FAMILIAL POSITION OF THE CAPE GENUS *EMPLEURIDIUM*[1]

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ABSTRACT

The monotypic southwestern Cape genus *Empleuridium* was assigned with doubt to Rutaceae when first described in 1860. Poorly known until recently, it has been rediscovered and new collections have made possible detailed studies of its embryology and reproductive anatomy; stem and leaf anatomy; and pollen. Results confirm that *Empleuridium* is misplaced in Rutaceae and it seems best referred to Celastraceae, in which it is unusual in its ericoid habit, small size, and unilocular ovary that develops into a follicle-like single-seeded fruit. The very small flowers have a floral disc in which the inferior ovary is embedded. Previous observations that *Empleuridium* was dioecious are incorrect; the flowers are perfect.

The monotypic genus *Empleuridium* was first described in 1860 and was based on a collection made by the early Cape collectors Ecklon and Zeyher in the 1820s. Publication was nearly simultaneous in "Flora Capensis" (Sonder, 1860) and in a series of illustrations, the "Thesaurus Capensis," intended to supplement the Flora (Harvey, 1859–1860). *Empleuridium* is usually attributed to Sonder, and the species *E. juniperinum* to Sonder & Harvey. It was assigned with doubt to Rutaceae by Sonder and has since remained in this family in generic floras of Southern Africa (Phillips, 1926, 1951; Dyer, 1975).

Empleuridium is a small shrub with needle-like leaves and small tetramerous flowers, the four stamens located at the edge of a floral disc and alternating with the petals. It is rare and apparently had not been recollected for over 120 years when Elsie Esterhuysen, the well known Cape botanist who has made a study of the Cape mountain flora, found plants growing on rocky mountain slopes at two localities in the southwestern Cape. She realized that her find was unusual and collected ample material, including a supply of specimens fixed in FAA. Subsequently, the first author suggested to her that the plants in question might be the poorly known *Empleuridium*. An examination of the type material at Stockholm (S), made by the Director, Dr. B. Nordenstam, confirmed this.

Empleuridium apparently does not belong in Rutaceae according to Dr. I. Williams (pers. comm.), who has revised several southern African genera of this family, including *Empleurum,* to which *Empleuridium* is superficially similar. Because the affinities of *Empleuridium* are not known, this study was undertaken in the hope of establishing more satisfactorily the relationships of the genus. Embryological and floral anatomy studies were made by Hiroshi Tobe; stem and leaf anatomy by Sherwin Carlquist; and pollen by Varsha Patel.

MATERIALS AND METHODS

Plants used in this study were collected in the wild and preserved in FAA. Voucher data is as follows: *Empleuridium juniperinum* Sonder & Harvey:

South Africa: Cape, Caledon district, above De Rust, 3,000 ft., *Esterhuysen 34318* (BOL, MO, RSA).

South Africa: Cape, Caledon district, upper slopes of Mt. Lebanon, 3,800 ft., *Goldblatt 6918* (MO).

Wood studies were supplemented with herbarium material of a portion of root (*Esterhuysen 34318*-RSA).

EMBRYOLOGY

For light-microscopic observations, FAA preserved flowers and fruits at various stages of development were dehydrated through a *t*-butyl alcohol series and embedded in Paraplast with a melting point of 56–58°C. Serial sections cut 5–10 μm thick were stained with Heidenhain's hematoxylin, safranin and fastgreen FCF, and were mounted in Canada Balsam. Electron-microscopic observations on seeds were also made following a standard technique and using JSM-25S (JEOL).

VEGETATIVE ANATOMY

Dried root material was boiled preparatory to further treatment. Prior to sectioning, both the

FAA and dry material were treated in ethylene diamine for softening in preparation for paraffin sectioning, a technique (Carlquist, 1982) in which small twigs or objects with both hard and soft portions can be sectioned successfully. A safranin-fast green combination was used for staining sections. Macerations were prepared with the aid of Jeffrey's fluid.

POLLEN

Buds containing pollen were treated by acetolysis (Erdtman, 1960), air dried from 95% ethanol, sputter coated with gold, and examined with an International Scientific Instruments Super II scanning electron microscope. Slides of glycerine jelly mounts were also examined with transmitted light using a Leitz Ortholux microscope.

OBSERVATIONS

FLORAL MORPHOLOGY

The flowers are solitary and borne in the axils of the needle-like leaves. The pedicels are 1.5–2 mm long at flowering, elongating up to 3 mm in fruit (Fig. 4). A pair of tiny opposed scaly bracts (Fig. 4) are present at the base of the pedicel. The flowers are small, 1.5–2 mm long and ca. 2 mm in diam.; perfect and tetramerous, comprising four sepals and four petals apparently arranged in whorls, but decussate in young buds (Fig. 2). There are four stamens and an ovary (Figs. 2, 3; see also Fig. 6) of probably four carpels (see next section). The stamens are alternate with the petals (Fig. 2), i.e., haplostemonous. Aestivation of the sepals and petals is imbricate (Fig. 2). The filaments are short, ca. 1 mm long. A style is also very short with a capitate stigma (Fig. 4). A nonnectariferous disc is slightly developed in the intrastaminal area. Both the sepals and the style are persistent.

The ovary is hemi-inferior and embedded in the receptacle (Fig. 1; see also Fig. 6A, B). The ovary is unilocular with four (occasionally three) erect ovules, and completely lacks the septa (Figs. 1, 3) that would represent the fused lateral walls

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FIGURES 1–5. Morphology and anatomy of flower and fruit of *Empleuridium.* se, sepal; pe, petal; st, stamen; ov, ovule; sc, scaly bract; pd, pedicel; fr, fruit coat; sd, seed.—1. Longitudinal section of a flower bud. Scale = 200 μm.—2. Transverse section (TS) of a flower bud at the level of anther. Note imbricate aestivation of sepals and petals. Scale = 100 μm.—3. TS of a flower bud at ovary level. Note the ovary is unilocular and occasionally contains only three ovules. Scale = 200 μm.—4. Fruit in various stages of development. The one on the right is nearly mature. Scale = 2 mm.—5. TS of a young fruit: the fruit is one-seeded and the fruit coat has no secretory cavities. Scale = 200 μm.
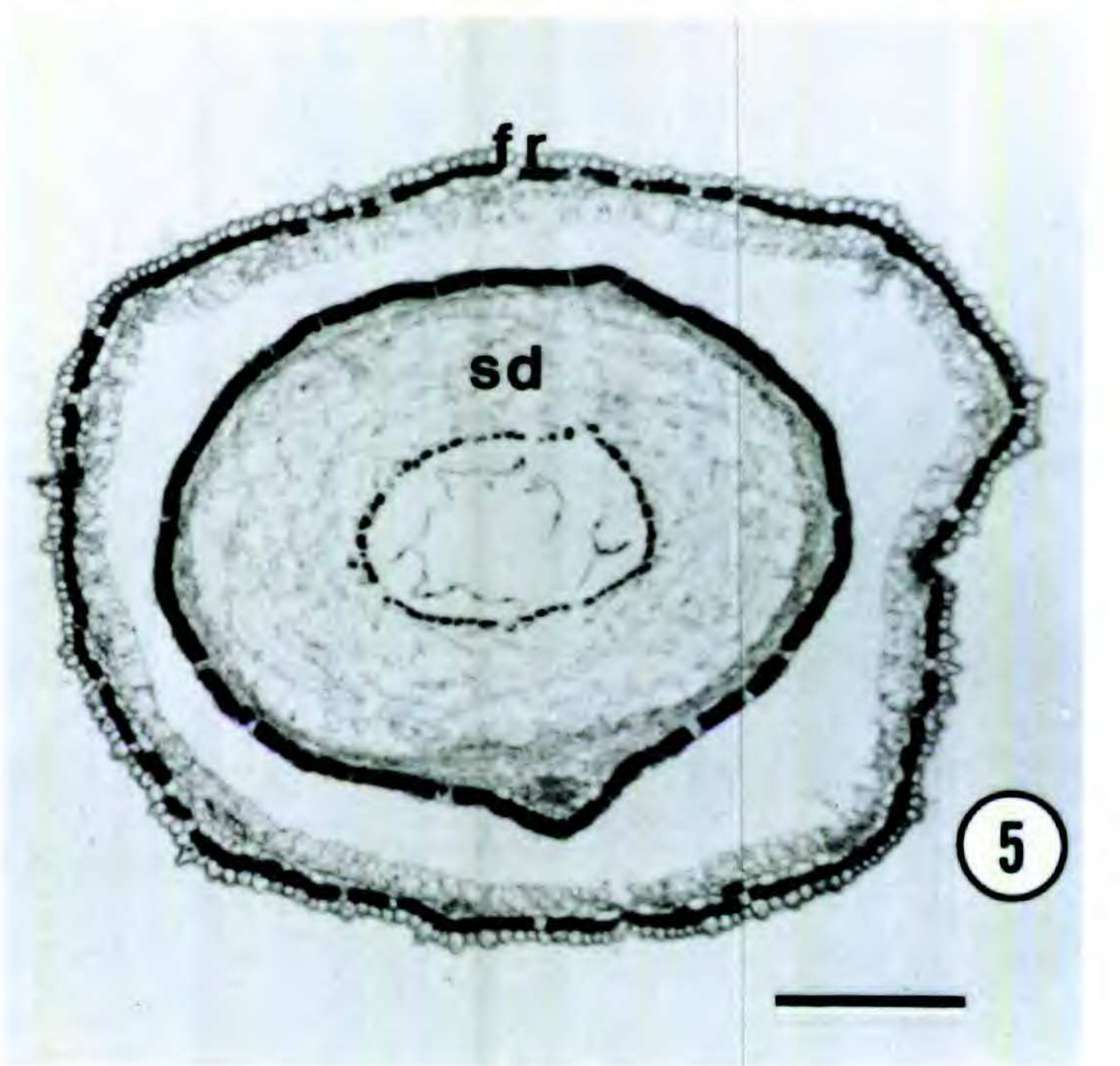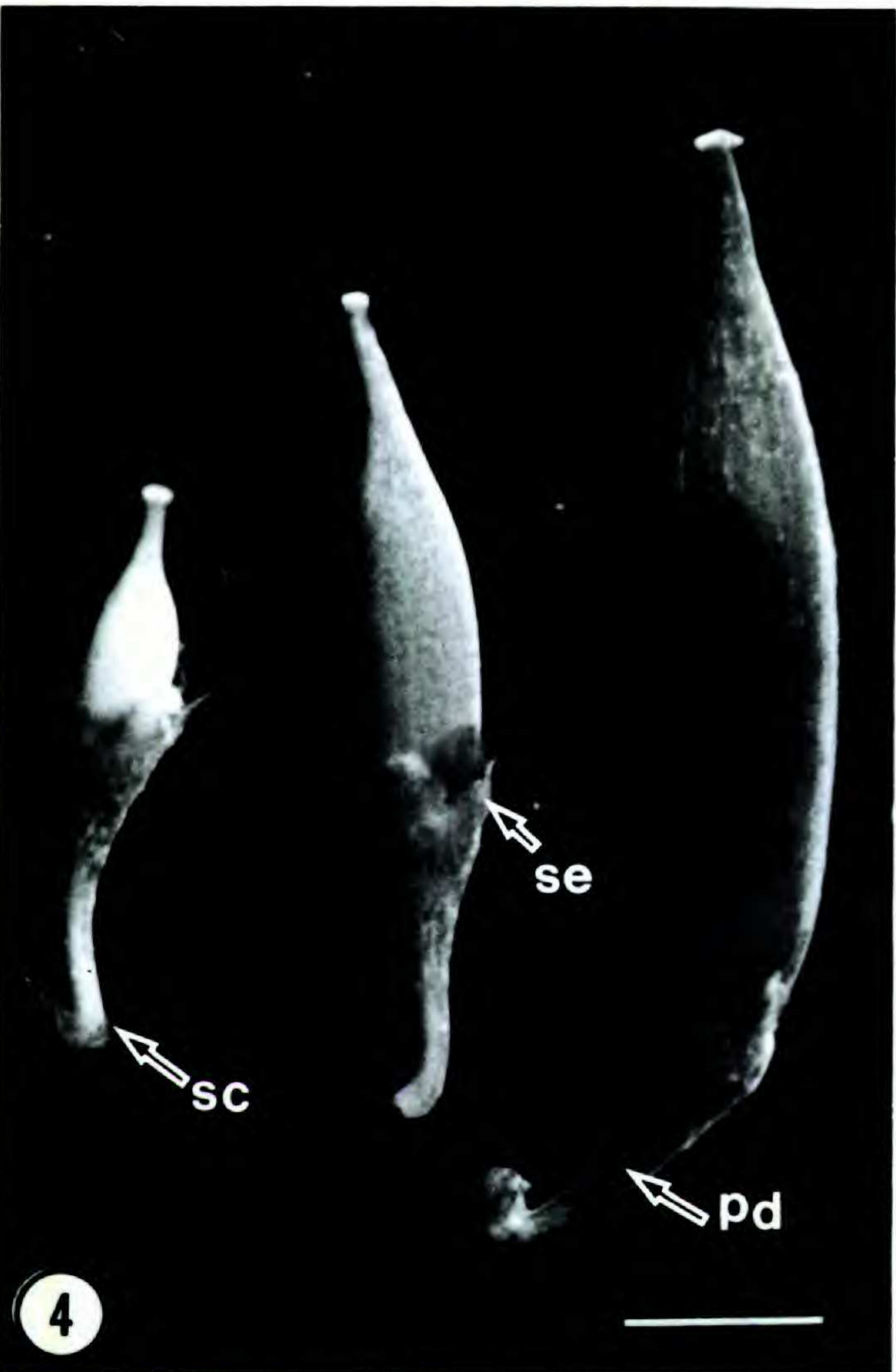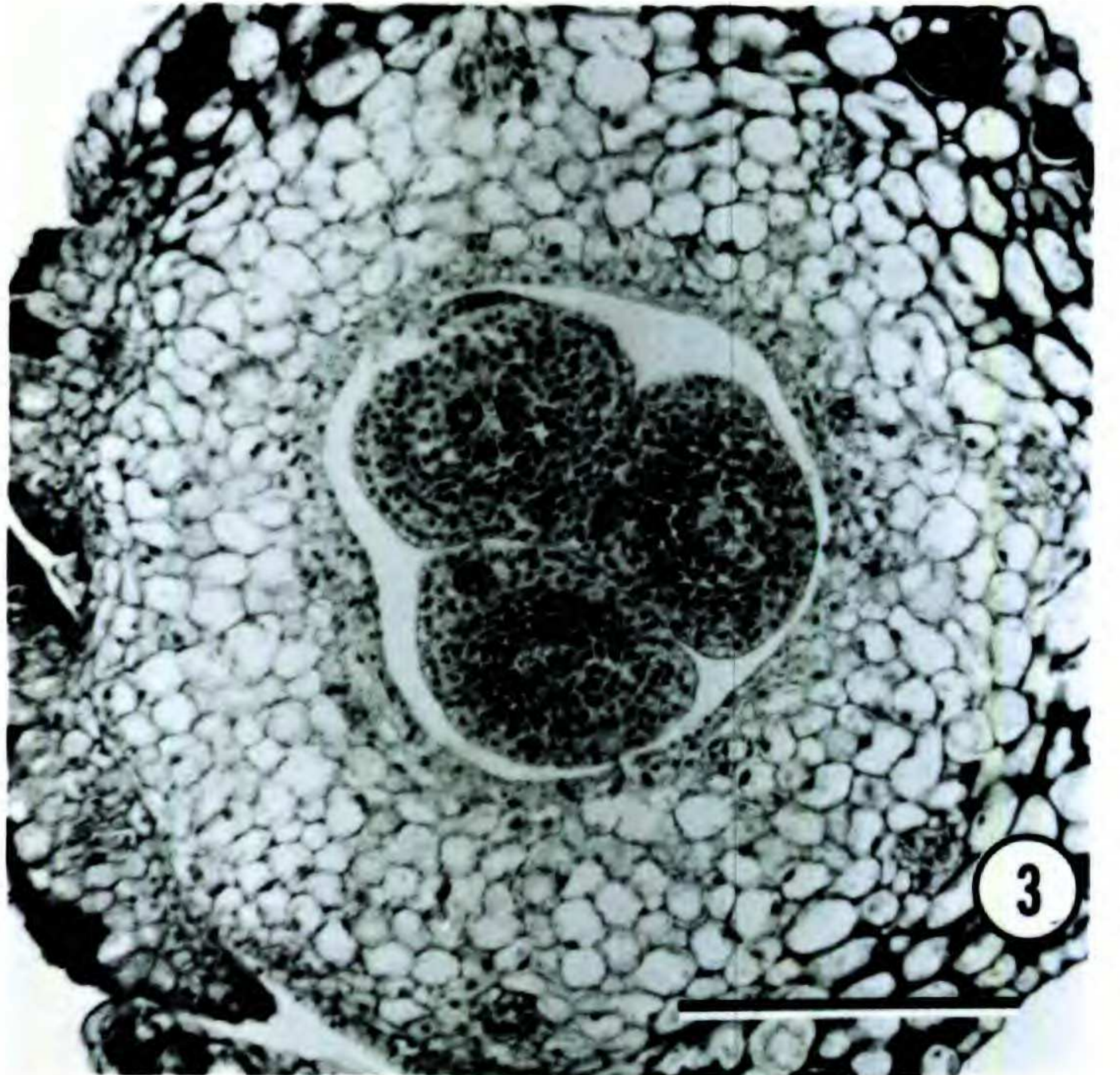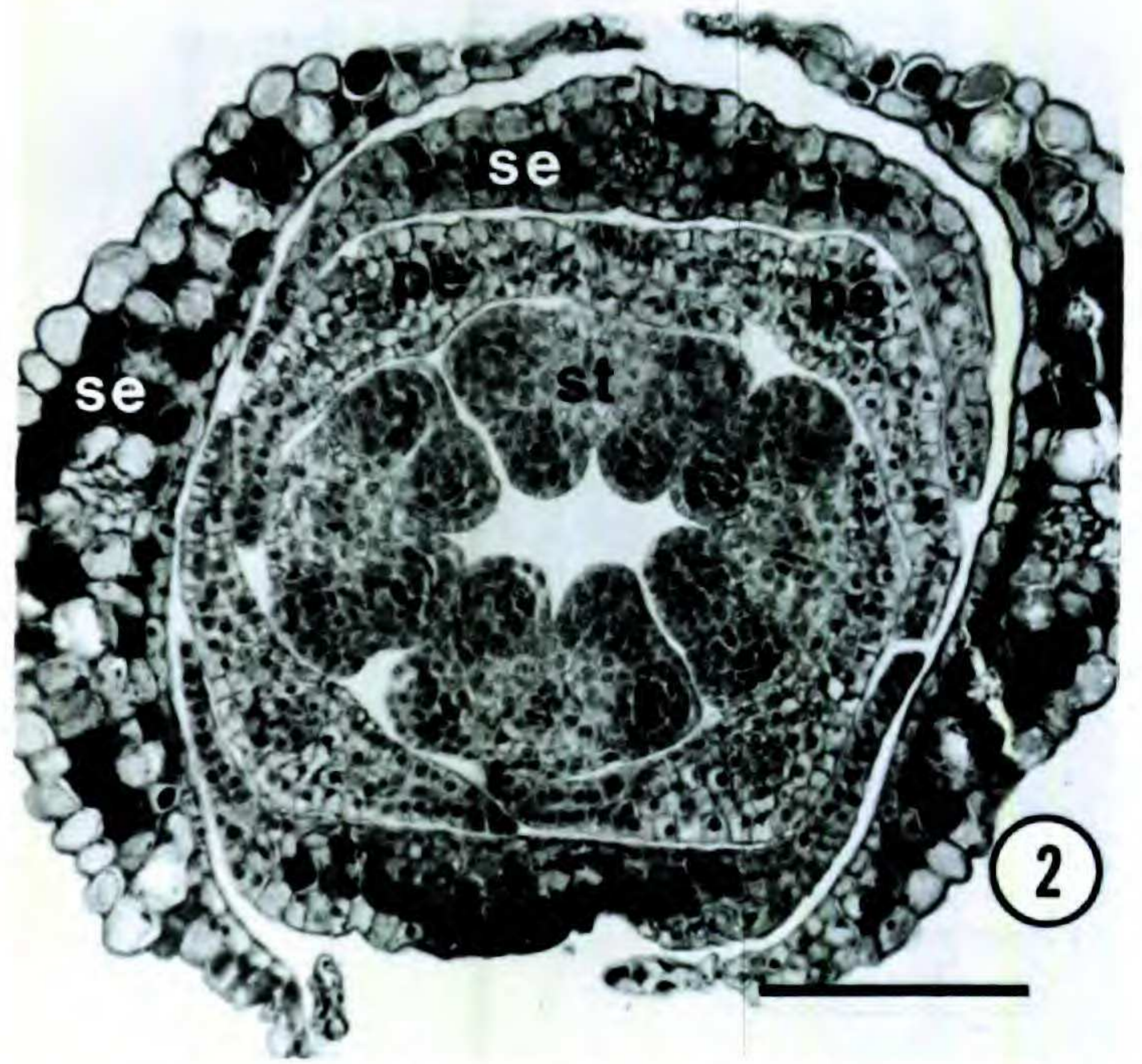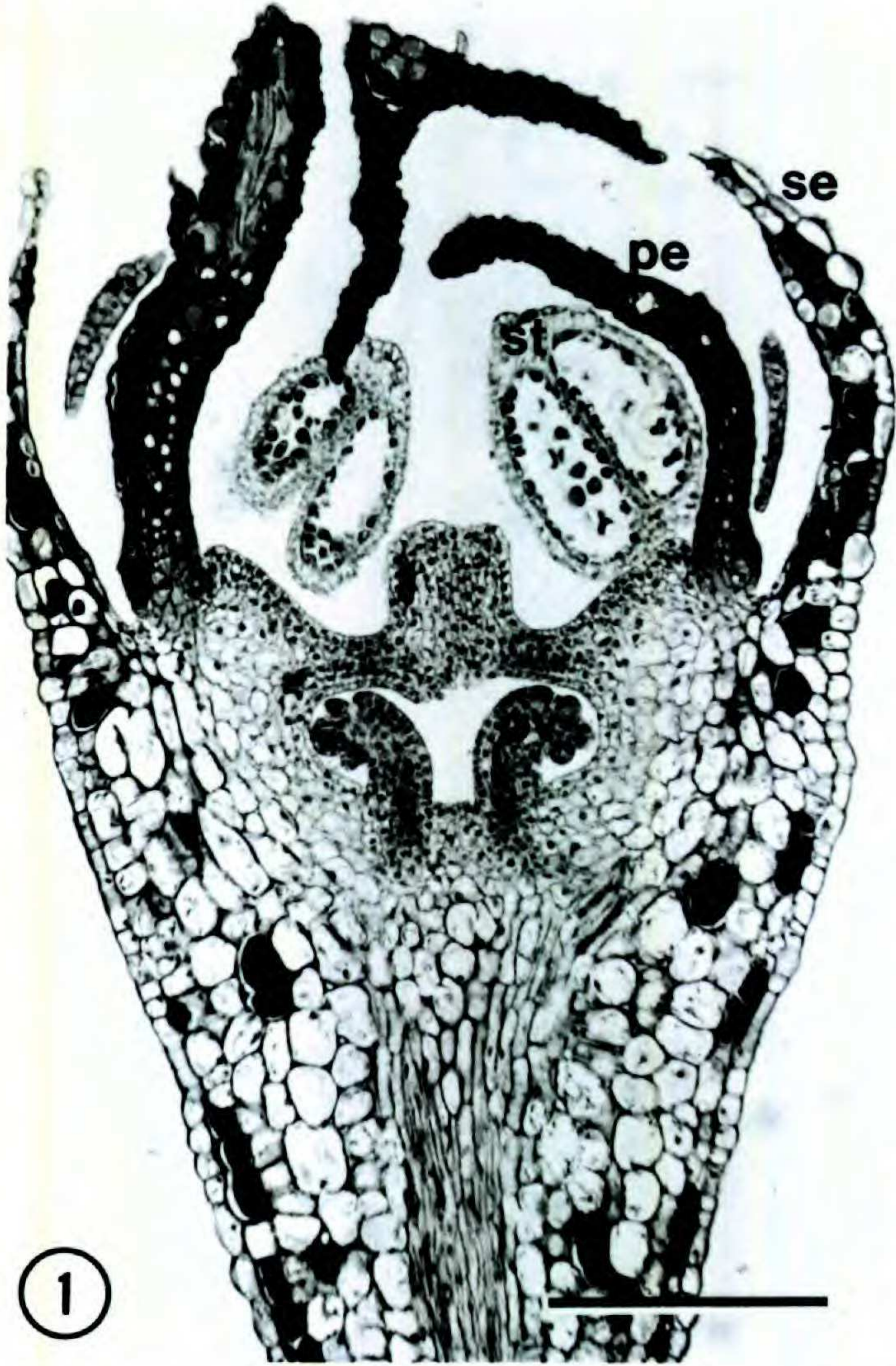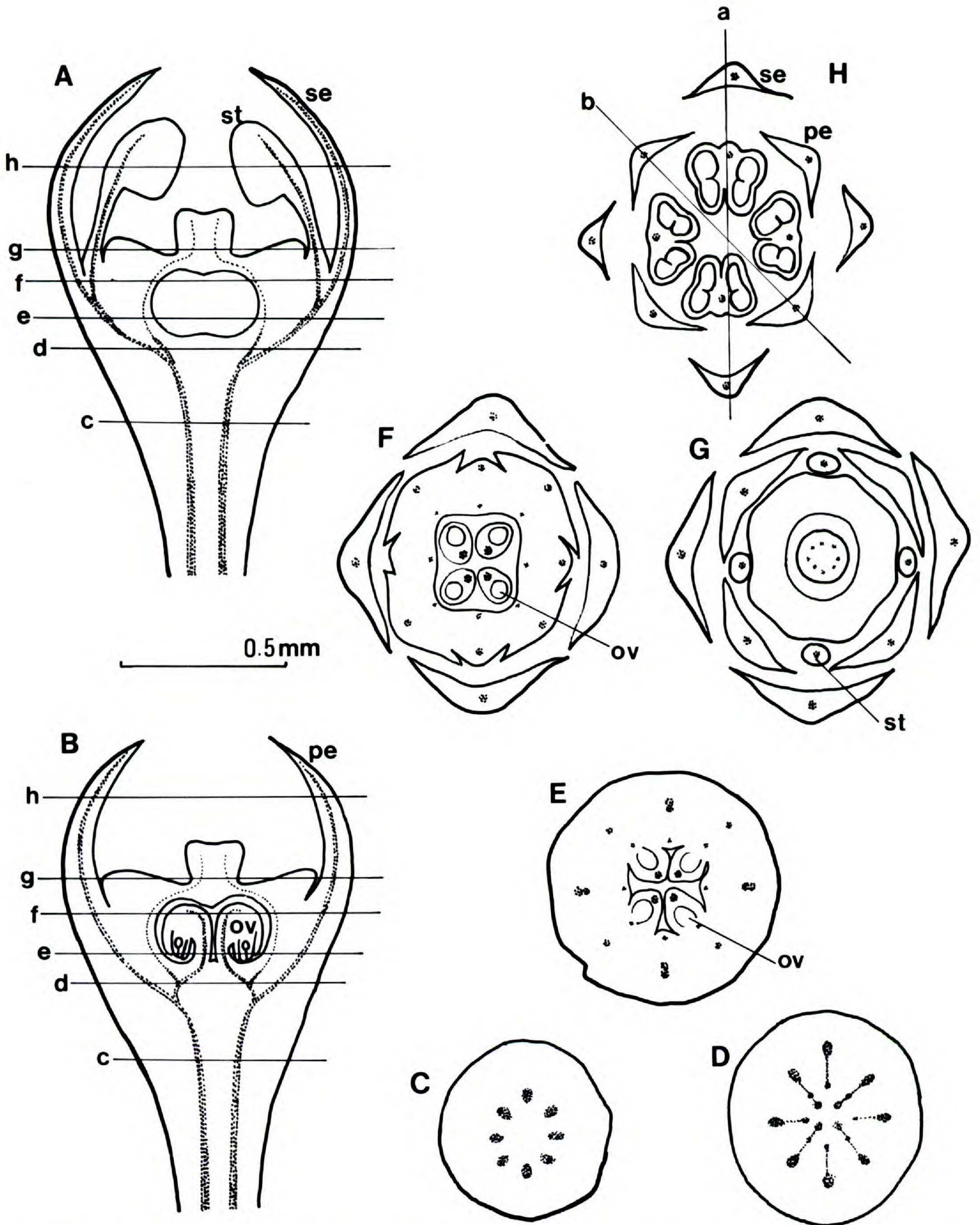
FIGURE 6.   Diagrams illustrating the floral anatomy and vasculature in *Empleuridium*. Symbols are the same as those in Figures 1–5.—A, B. Median longitudinal sections of a flower through the line marked a and b in H.—C–H. Transverse sections of a flower at levels marked c–h in A and B.

of the constituent carpels. The ovules are alternate to the stamens (see Fig. 6F). Placentation is basal (Figs. 1, 6B).

Although the ovary is initially inferior, it elongates beyond the level of the stamens after fertilization (Fig. 4). At maturity all but a tiny part of the fruit extends beyond the receptacle. The fruit is 7–9 mm long, fusiform and slightly curved with a tapering persistent style. It is always one-seeded (Fig. 5) and is follicle-like, although strictly a capsule since it is derived from a compound ovary. The fruit wall is thin and consists of four to five cell layers and lacks secretory cavities expected in Rutaceae. The large, black seed has a distinctive white aril or elaiosome at the base which has several thread-like coiled extensions. This is described in more detail in a later section.

FLORAL ANATOMY

Vasculature of the flower is very simple, and does not form a network by mutual fusions of vascular bundles in the receptacle. At the basal part of the receptacle there are eight discrete (collateral) bundles (Fig. 6C), each supplying the vascular traces to either a sepal/stamen or a petal/particular ovary-wall part/ovule, depending on the dispositional relationship between the vascular bundle and appendages (Fig. 6D–H). The sepals, petals, and stamens each have a single bundle (Fig. 6H). In the wall of the inferior ovary there are eight small vascular bundles that extend upward into a short style (Fig. 6E, G). Vascular strands entering the four ovules are separately derived from the four vascular bundles, which are opposite the four petals respectively, and each of which emits traces not only to a petal but also to the dorsal part of the ovary wall.

The vascular anatomy suggests that the four ovules in the single ovary are originally those of four carpels. It seems that the unilocular hemi-inferior ovary of *Empleuridium*, containing four ovules evolved from a four-carpellate, septate compound ovary by loss of septa.

VEGETATIVE ANATOMY

Wood (Figs. 7–12). Wood of stems (Figs. 7, 8) is described first here; features by which root wood differs follow. Stem wood with occasional vague growth rings demarcated by wider vessels in earlywood. Vessels are angular to rounded in transectional view; mean vessel diam., 15 μm; mean vessel wall thickness, 1.4 μm. Mean number of vessels per sq. mm is 844. Mean vessel element length, 136 μm. Perforation plates simple, a few with a transverse bar. Lateral walls of vessels with alternate or scalariform pitting. Imperforate tracheary elements all tracheids with fully bordered pits. Mean tracheid wall thickness, 3 μm; mean tracheid length, 282 μm. Axial parenchyma sparse, vasicentric (because of vessel abundance, contact of axial parenchyma is virtually inevitable), axial parenchyma in strands of two cells. Rays few, uniseriate, all composed of markedly erect cells; the wood appears nearly rayless (Fig. 8). Wood non-storied.

Wood of root like that of stem except for the following features. Root wood with little growth ring activity (Fig. 9). Mean vessel diam., 25 μm; mean vessel wall thickness, 2.5 μm. Mean number of vessels per sq. mm is 494. Mean vessel element length, 316 μm. Perforation plates simple (Fig. 11) or with one to three bars (Fig. 12). Lateral walls of vessels with alternate pits or pits which may be provisionally termed scalariform (Fig. 11). Mean wall thickness of tracheids, 4.6 μm; mean tracheid length, 520 μm. Wood nearly rayless (Fig. 10), an occasional uniseriate ray composed of erect cells present.

Node, cortex, and phloem. Nodes of *Empleuridium juniperinum* are all unilacunar with a single trace. The cortex is composed wholly of parenchyma cells except for a few scattered protophloem fibers in stems; fibers absent in roots (Fig. 15). Scattered tannin-bearing idioblasts and druse-bearing idioblasts present in both roots and stems (Fig. 15). Periderm present on root and lower portions of stems, originating in the first subepidermal layer. Some phloem parenchyma cells are subdivided into strands of crystal-containing cells; the crystals are single and rhomboidal, or few per cell, but are not aggregated into druses as in cortical cells.

Leaf. Although linear, the leaf is slightly flattened as seen in transection (Fig. 13). Stomata are ranunculaceous and present on all portions of the leaf surface. A thick cuticle is present and is raised into an overarching hood external to stomata (Fig.16). Chlorenchyma is two or three layers thick; cells are only a little longer than wide, are closely packed, and are not differentiated into palisade cells. Some chlorenchyma cells contain tannin, and an occasional druse-containing cell may be observed. Only a single main vein is present; a small veinlet may branch from this on either side. The main vein consists
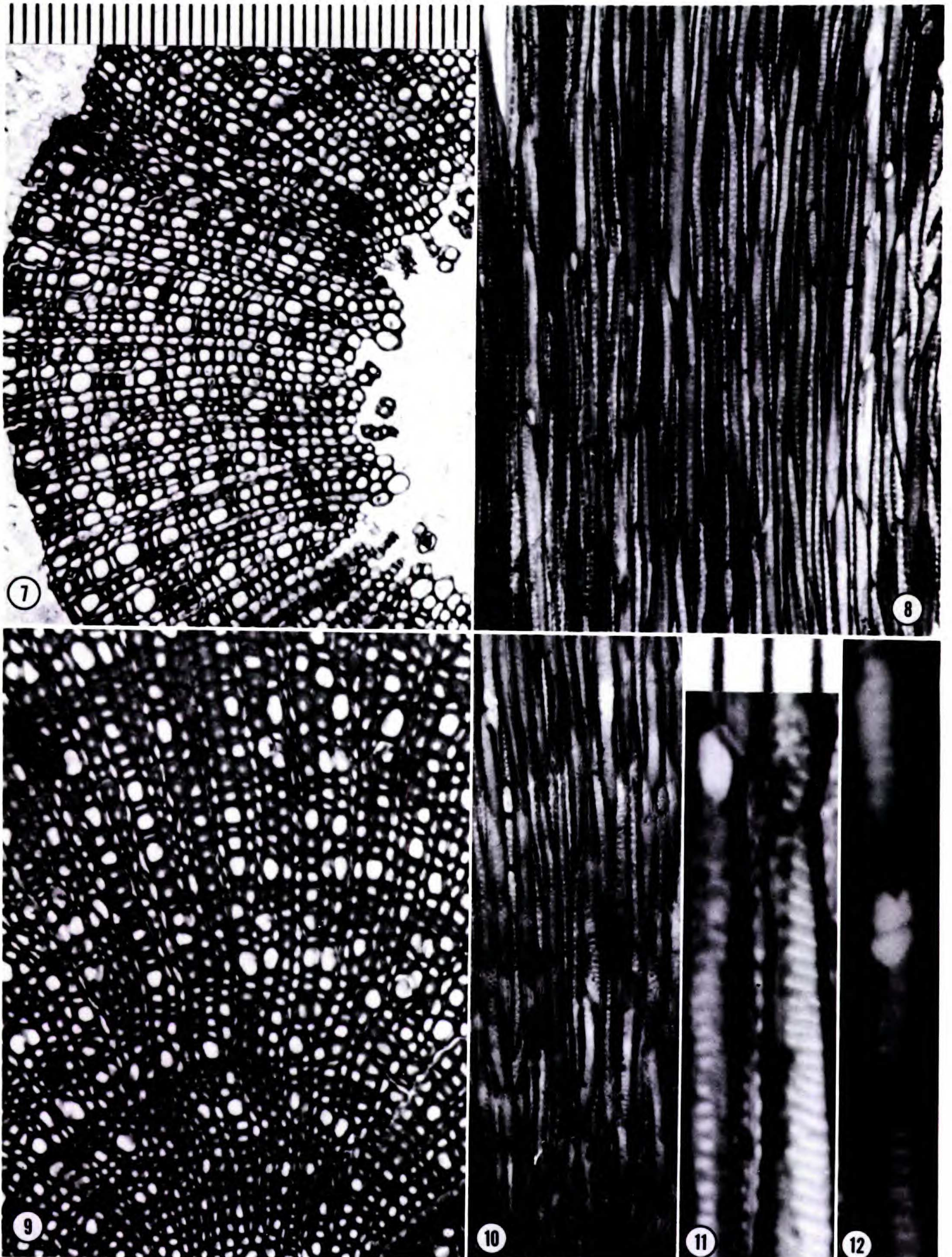
FIGURES 7–12.   Wood sections of *Empleuridium*. 7, 8. Stem, from *Goldblatt 3418* (MO).—7. Transection, cambium at left, pith at right.—8. Tangential section. A few elongate ray cells may be seen. 9–12. Root, from *Esterhuysen 34318* (RSA).—9. Transection, tracheids are thicker walled than in stem.—10. Tangential section. A single ray is present, upper left. 11, 12. Vessels from radial section.—11. Simple perforation plate (upper left); scalariform lateral wall pitting (right).—12. Perforation plate traversed by a single bar. Figures 7–10, scale above Figure 7 = 10 μm; Figures 11, 12, scale above Figure 11 = 10 μm.
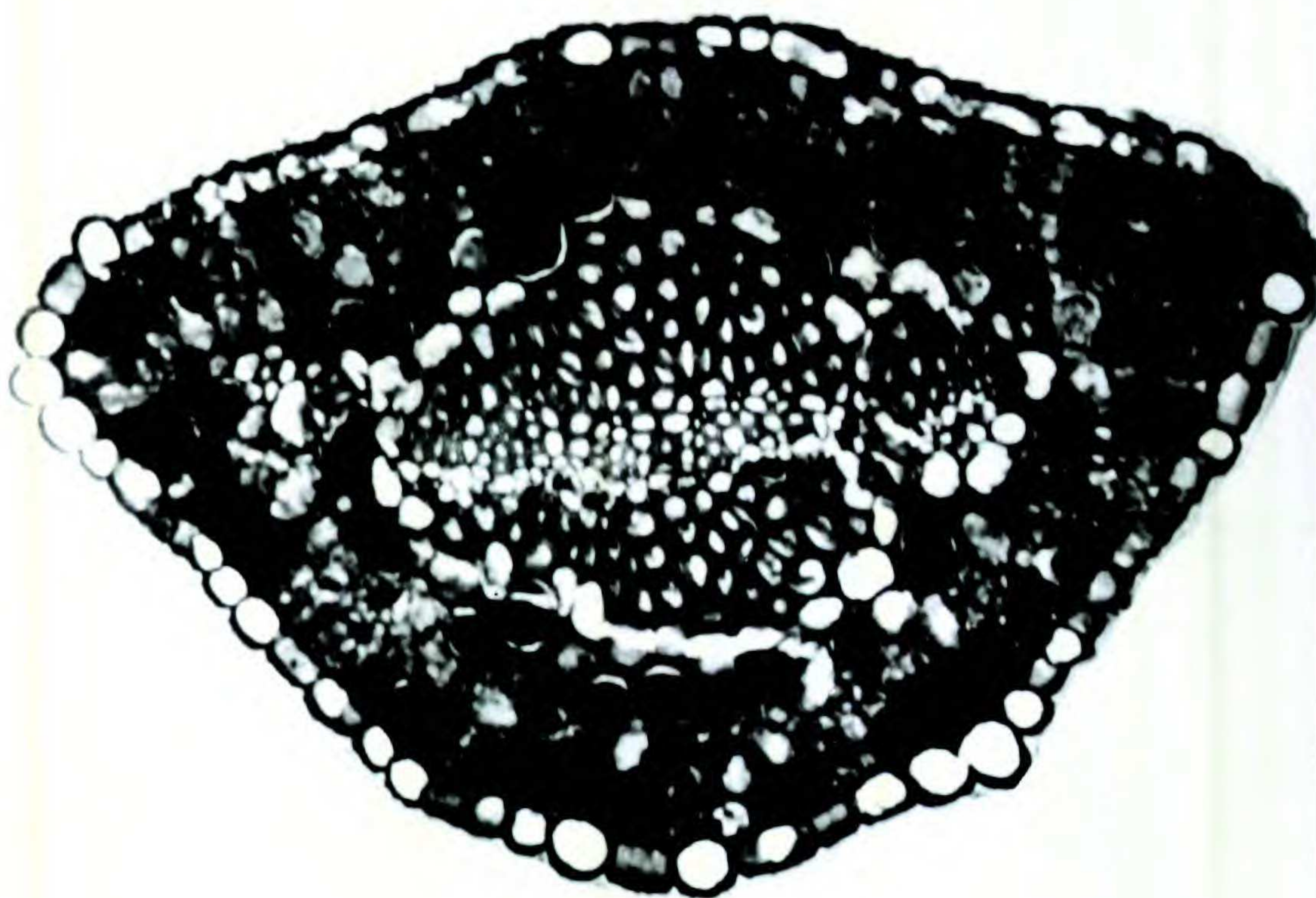
FIGURES 13–16. Sections of *Empleuridium*. 13, 14, 16, sections of leaf from *Goldblatt 3418* (MO).—13. Leaf transection, adaxial surface above.—14. Longitudinal section of vein in leaf; tracheids with scalariform and alternate circular pits at right, fiber at left.—15. Transection of cortex of root, from *Esterhuysen 34318* (RSA). Druses visible in some cells, tannin in others; periderm at right.—16. Stoma from leaf, showing overarching cuticular ridges. Figures 13, 15, scale above Figure 7; Figures 14, 16, scale above Figure 11.
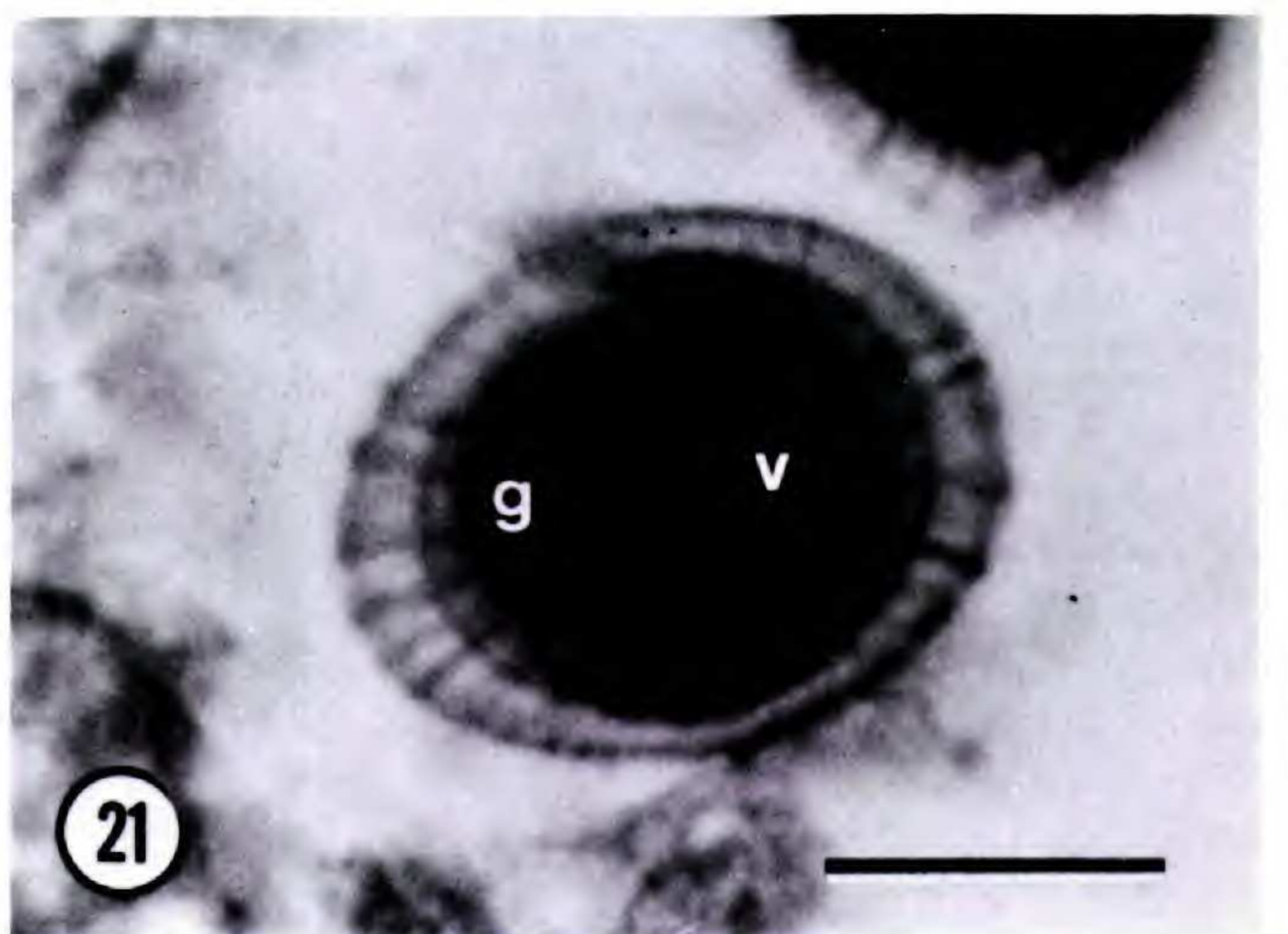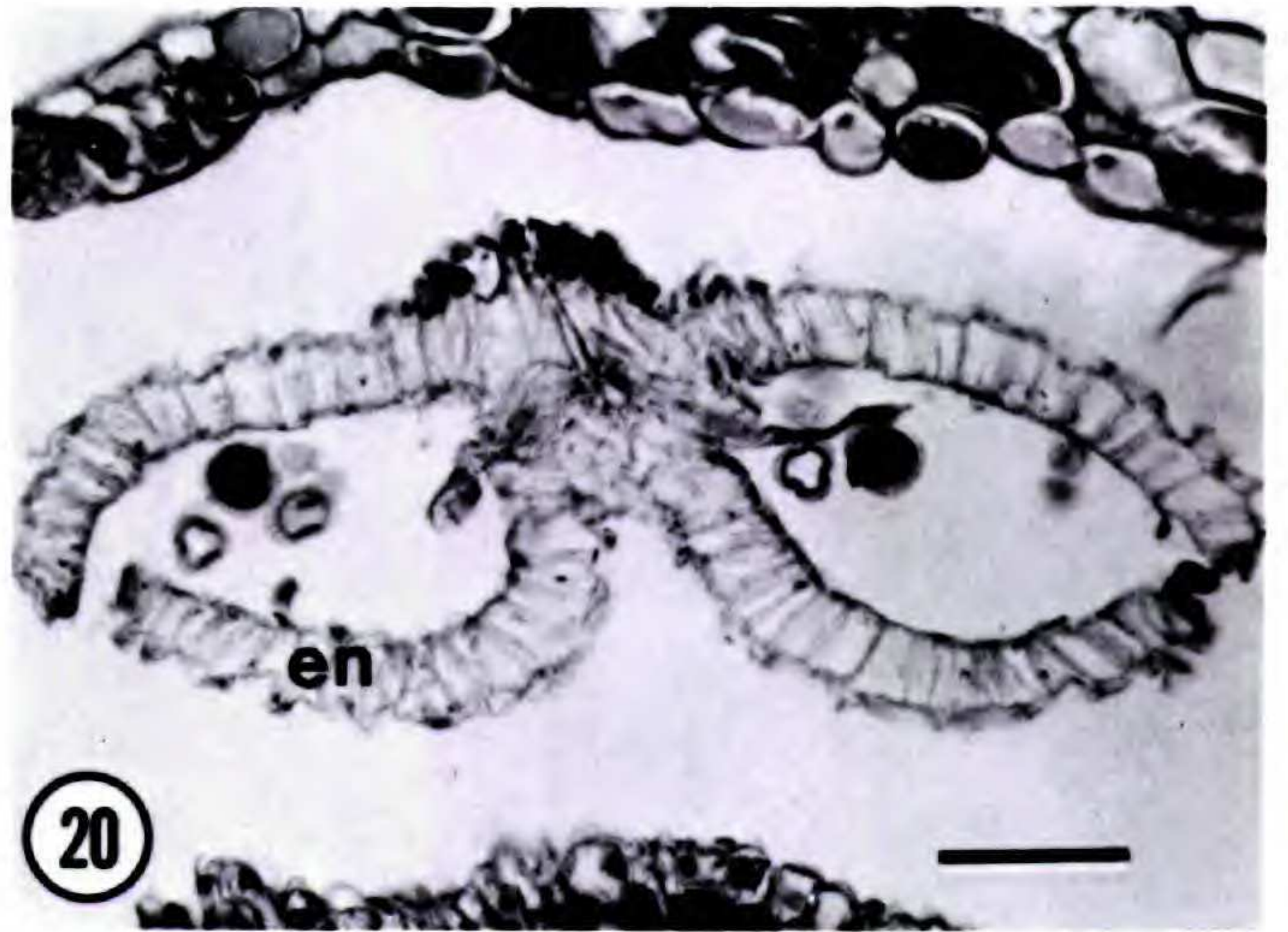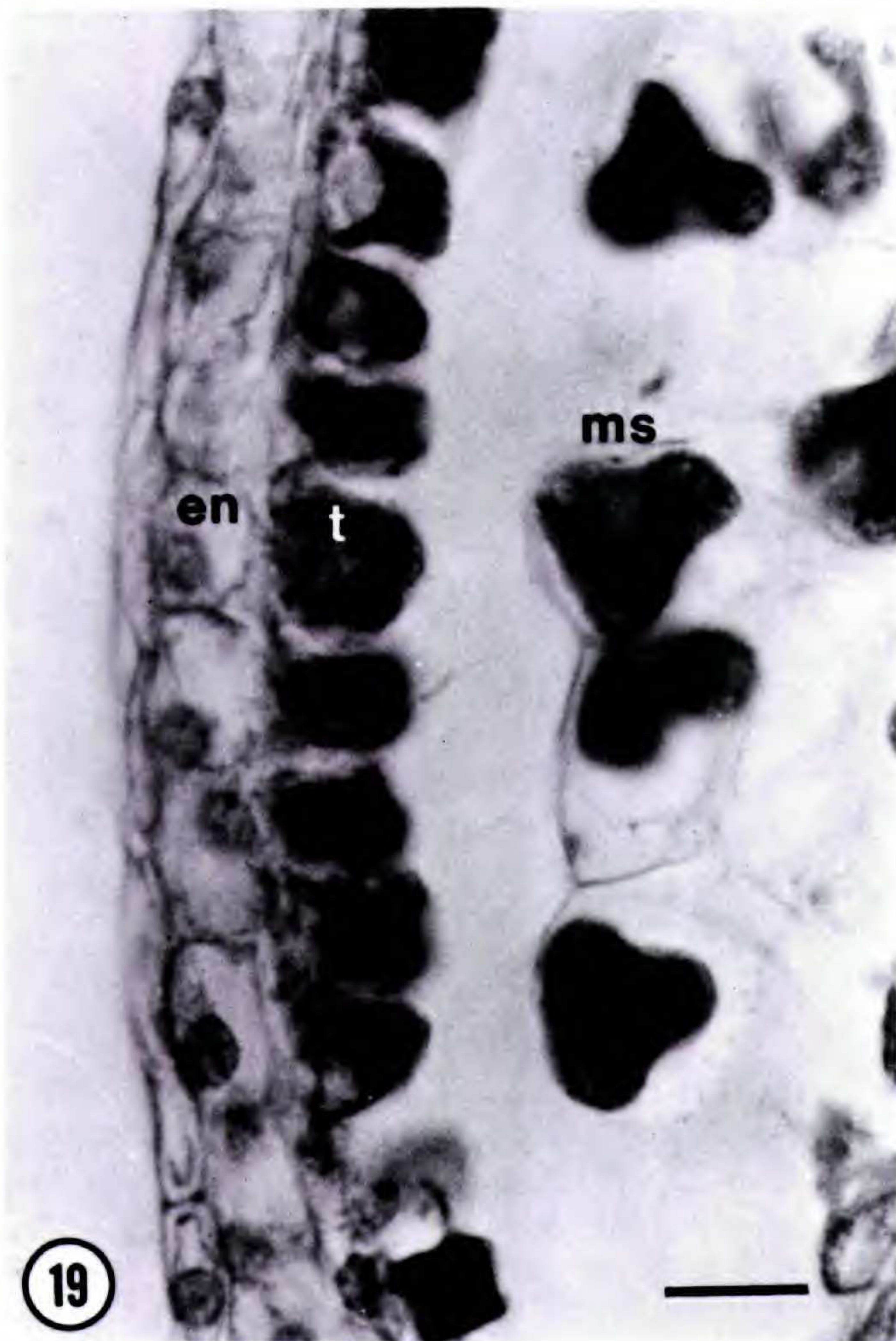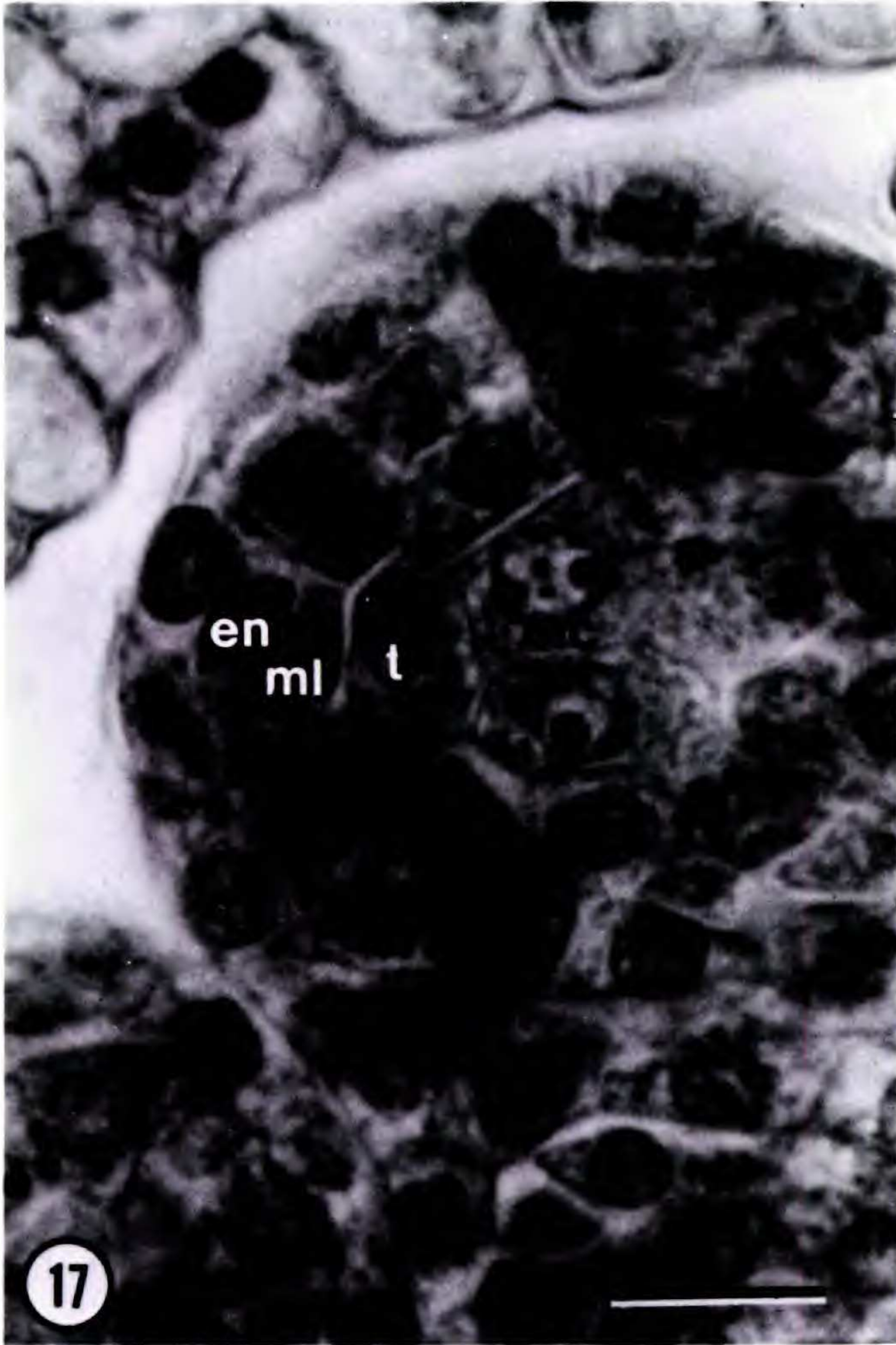
of a laterally wide bundle sheathed adaxially and abaxially by fibers. The xylem of the vein consists of annular, helical, and scalariformly pitted tracheids, but also tracheids with circular bordered pits (Fig. 14, right). No secretory cavities were observed.

EMBRYOLOGY

Anther and microspores. The anther is tetrasporangiate. The wall structure prior to maturation comprises four layers; epidermis, endothecium, one middle layer, and tapetum (Fig. 18). Cells of the middle layer and endothecium are derived from the same cells (Fig. 17), and the wall formation is regarded as conforming to the dicotyledonous type (Davis, 1966). During maturation, the epidermis mostly collapses and the middle layer degenerates while the endothecium develops fibrous thickenings. The tapetum is glandular and its cells become two-nucleate (Fig. 19) and finally degenerate. Thus the mature anther wall at dehiscence consists principally of the fibrous endothecium (Fig. 20). Dehiscence is longitudinal.

Meiosis in microspore mother cells is accompanied by simultaneous cytokinesis (Fig. 19). The shape of the microspore tetrads, on the basis of the examination of 50 selected tetrads, is usually (94%) tetrahedral and very occasionally (6%) decussate (expressions for the frequency follow Schmid, 1982). Pollen grains are released singly and are two-celled (Fig. 21).

Megagametophyte and nucellus. The ovule is anatropous and tenuinucellate. A single archesporial cell differentiates beneath the apical dermal layer of the small nucellus (Fig. 22), and directly develops into a megaspore mother cell (Fig. 23). No case was observed in which two or more archesporial cells were borne in a single nucellus. The megaspore mother cell normally undergoes meiosis, resulting in a linear or T-shaped tetrad of megaspores (Fig. 24). The chalazal megaspore of the tetrad always functions and successively develops into a two- (Fig.

25), four- (Figs. 26, 27), and eight-nucleate *Polygonum*-type embryo sac. The synergids exhibit no particular specialization. Two polar nuclei are united into a central nucleus before fertilization (Fig. 28). The three antipodal cells are ephemeral and always absent in the organized mature embryo sac. Thus prior to fertilization, the embryo sac consists only of an egg, two synergids, and the central nucleus (Fig. 28).

During megasporogenesis and megagametogenesis, a remarkable breakdown of the nucellar tissue surrounding the megaspores or the embryo sac occurs (Fig. 24). As a result, the greater part of the embryo sac after the two- or four-nucleate stage is no longer enclosed by the nucellar tissue but borders directly on the inner integument (Figs. 25–28). The break-down of the remaining nucellar tissue continues until it almost disappears. In a young seed, the enlarged embryo sac is wholly surrounded by the inner integument alone. No hypostase is formed during the development of the ovule and seed.

Integuments and endothelium. The micropyle is formed by the inner integument alone (Fig. 29). Both the inner and the outer integuments are initiated by involving an oblique-periclinal or periclinal division of dermal cells in an ovule primordium (see arrows in Fig. 30). The subsequent growth of the integument takes place by the division of cells derived from the dermal initials, while the subdermal cells do not contribute to the formation of the integuments. The integuments are thus regarded as being of "dermal origin" (Bouman & Calis, 1977). As early as the megaspore mother cell stage both the integuments are usually three cell-layers thick. In older stages, the constituent cells further divide periclinally, so that the outer integument becomes four cell-layers thick while the inner integument increases the thickness into more than six cell-layers. Neither the outer nor the inner integument is vascularized. A vascular bundle in the funiculus ends at the chalaza and does not exhibit post-chalazal branching.

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FIGURES 17–21. Development of anther walls and microspores in *Empleuridium*. ep, epidermis; en, endothecium; ml, middle layer; t, tapetum; mc, microspore mother cell; ms, microspores in telophase of meiosis II; v, nucleus of the vegetative cell; g, nucleus of the generative cell.—17. Transverse section (TS) of a young anther. Scale = 10 μm.—18. TS of an older anther than that shown in Figure 17. Scale = 10 μm.—19. TS of an older anther than that shown in Figure 18. Scale = 10 μm.—20. TS of a mature anther. Note that the wall comprises the fibrous andothecium alone. Scale = 100 μm.—21. Section of a mature pollen showing the two-celled state at the time of shedding. Scale = 10 μm.
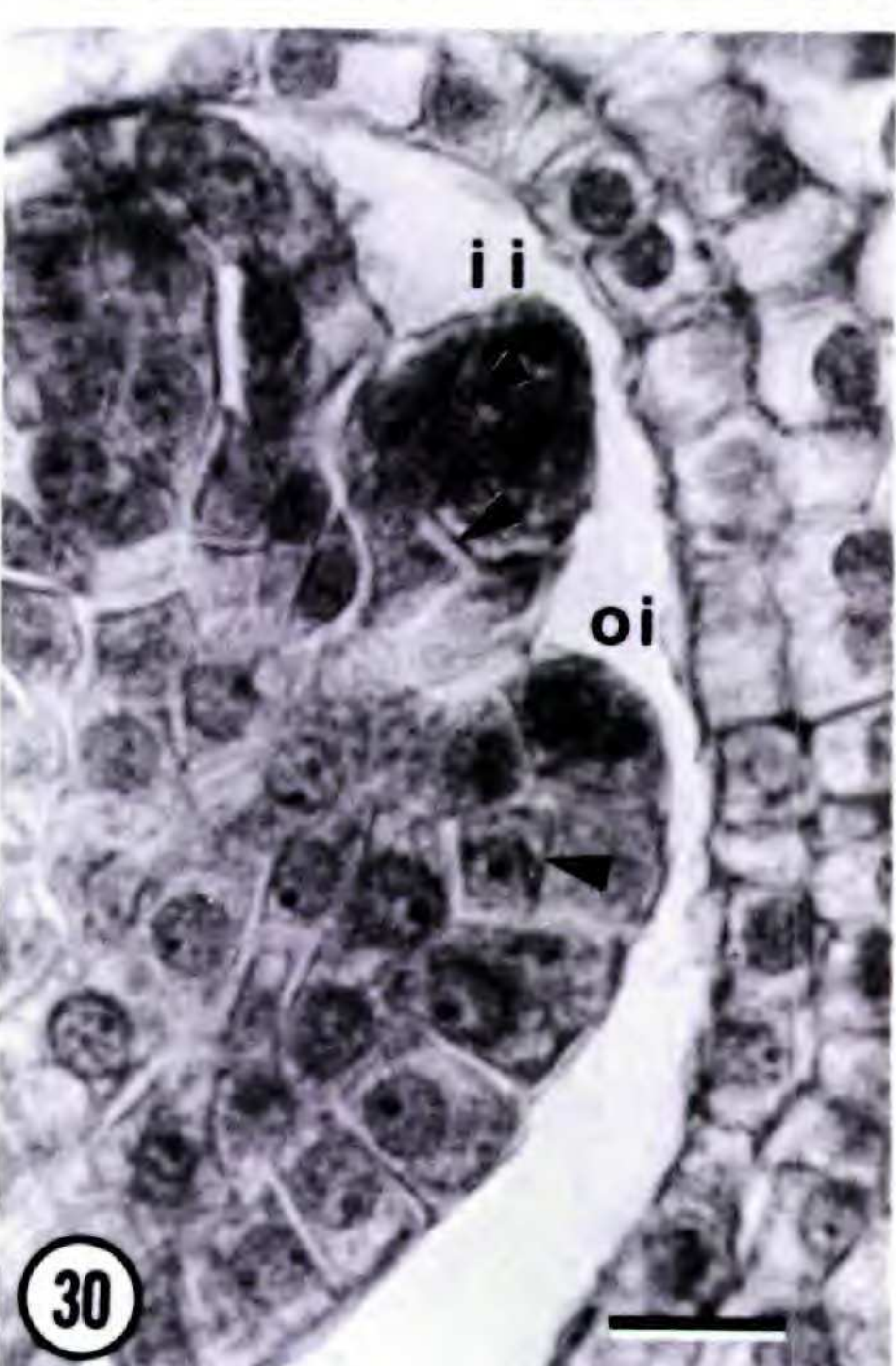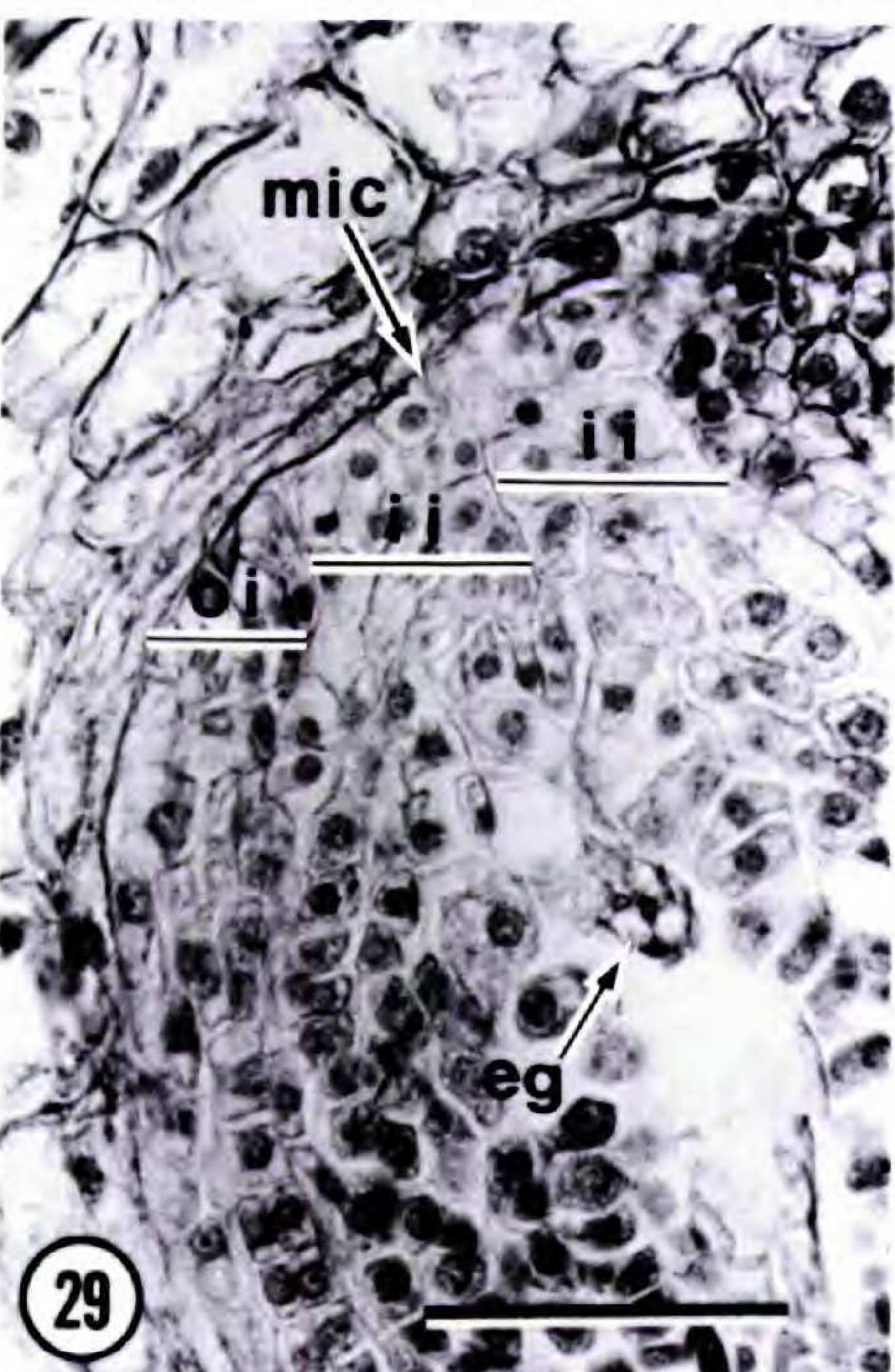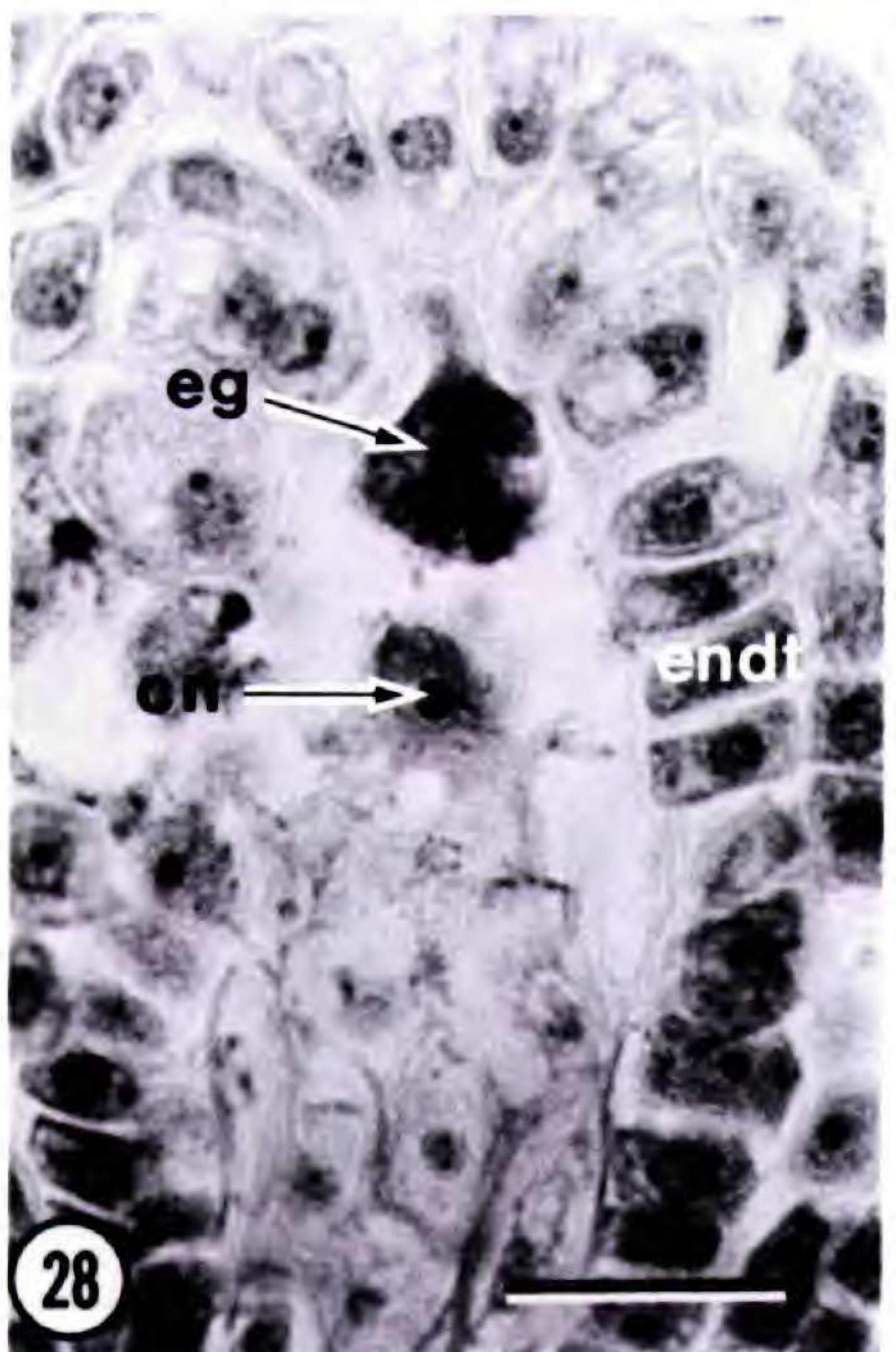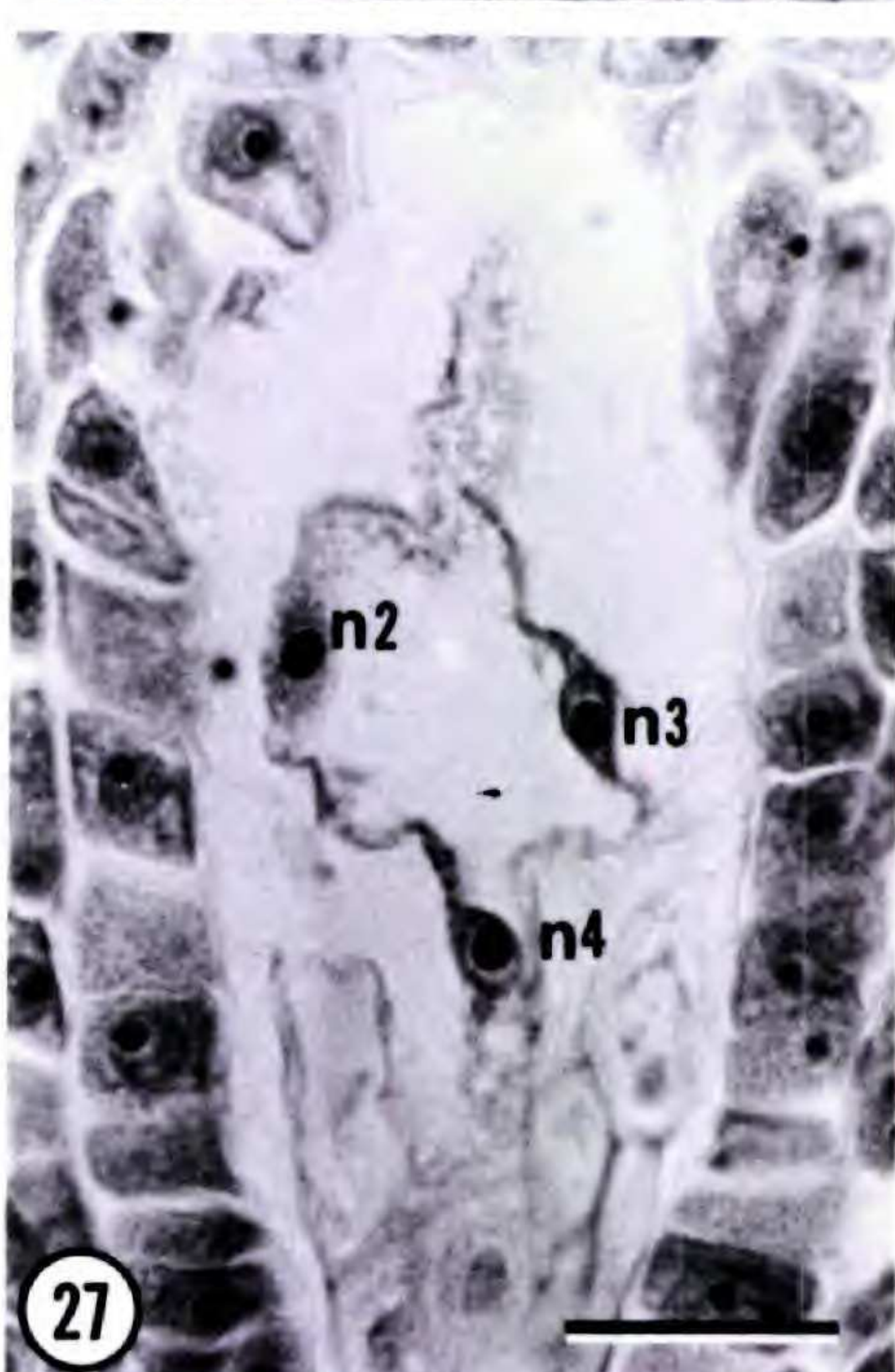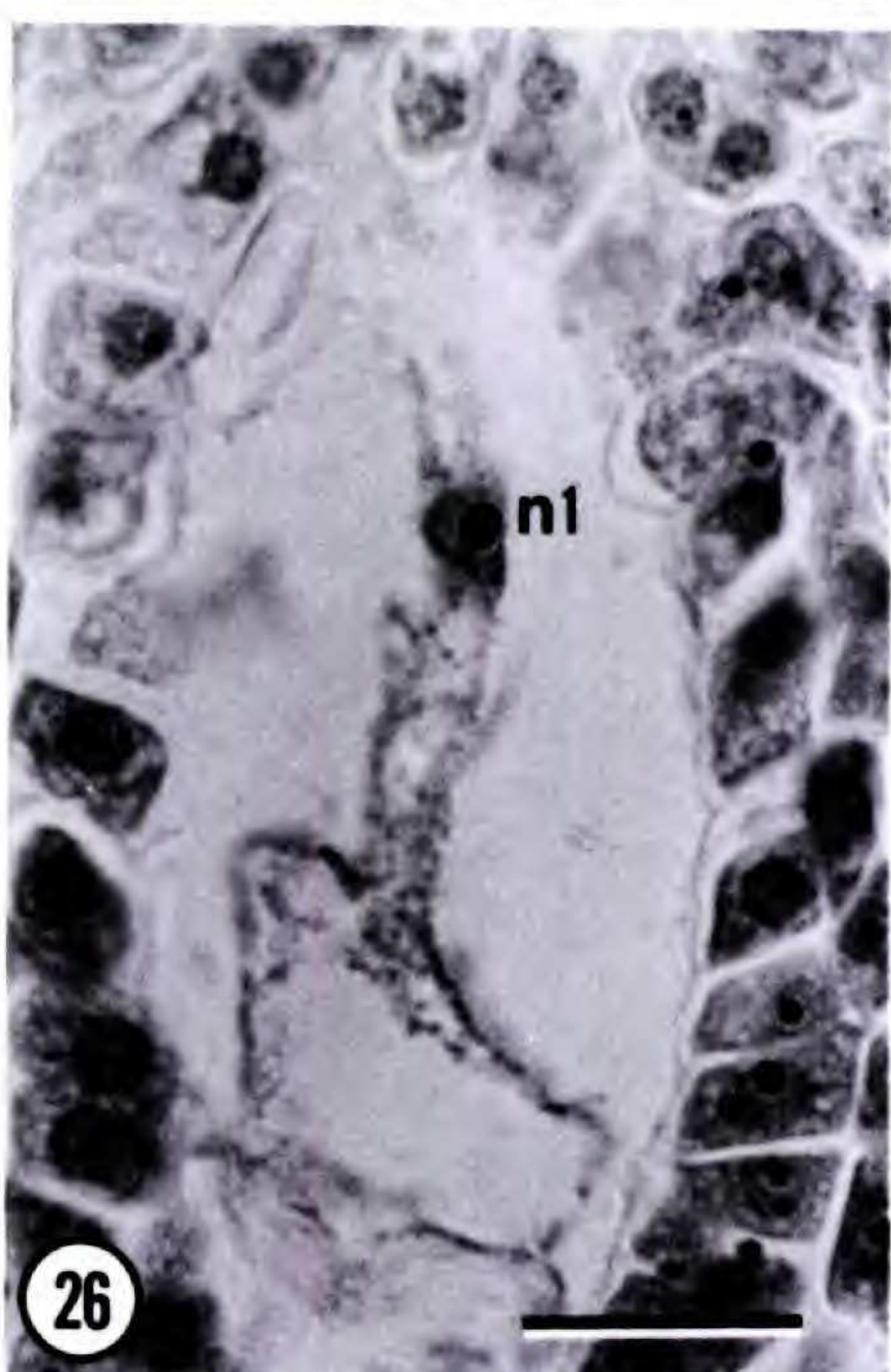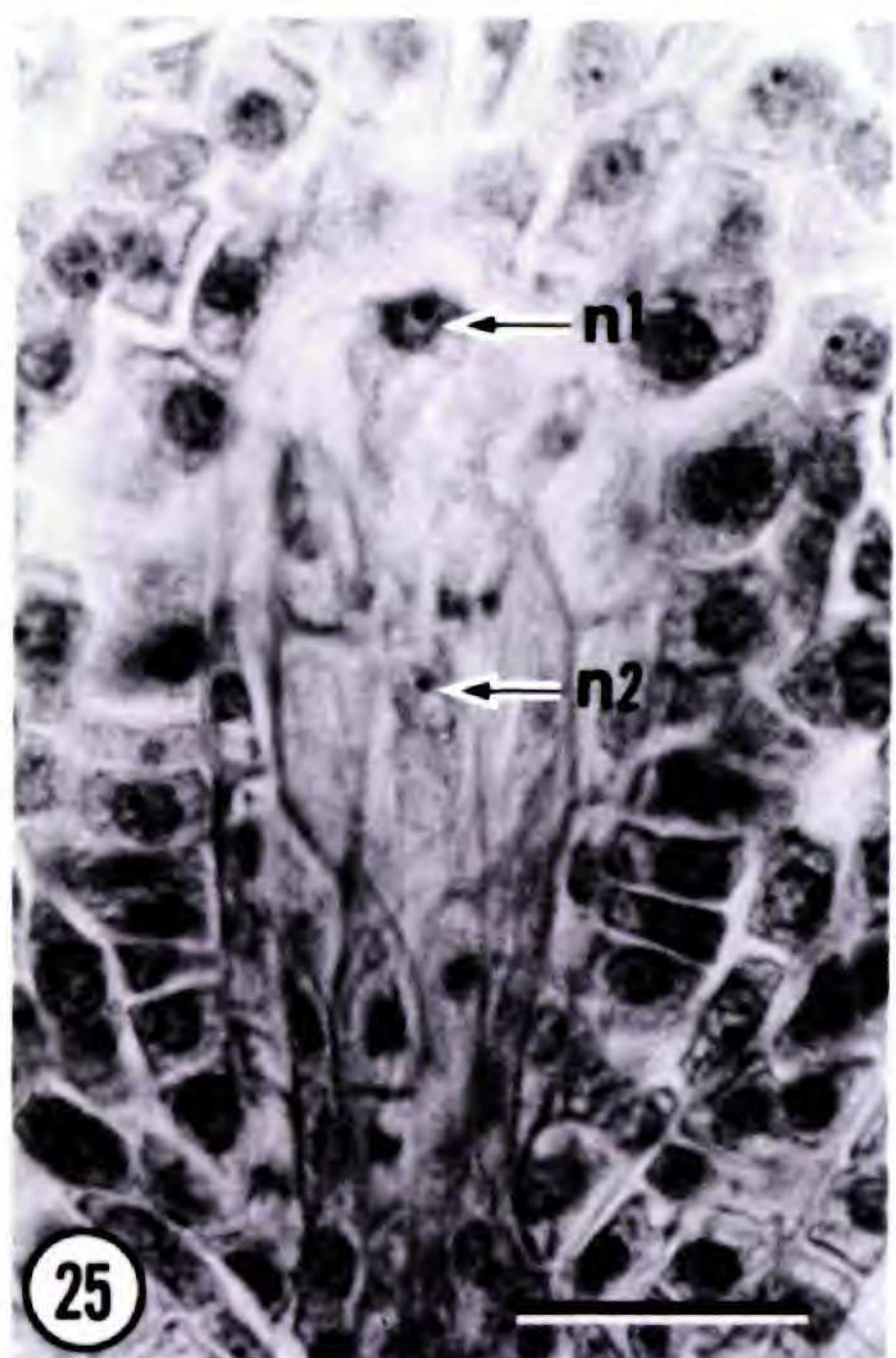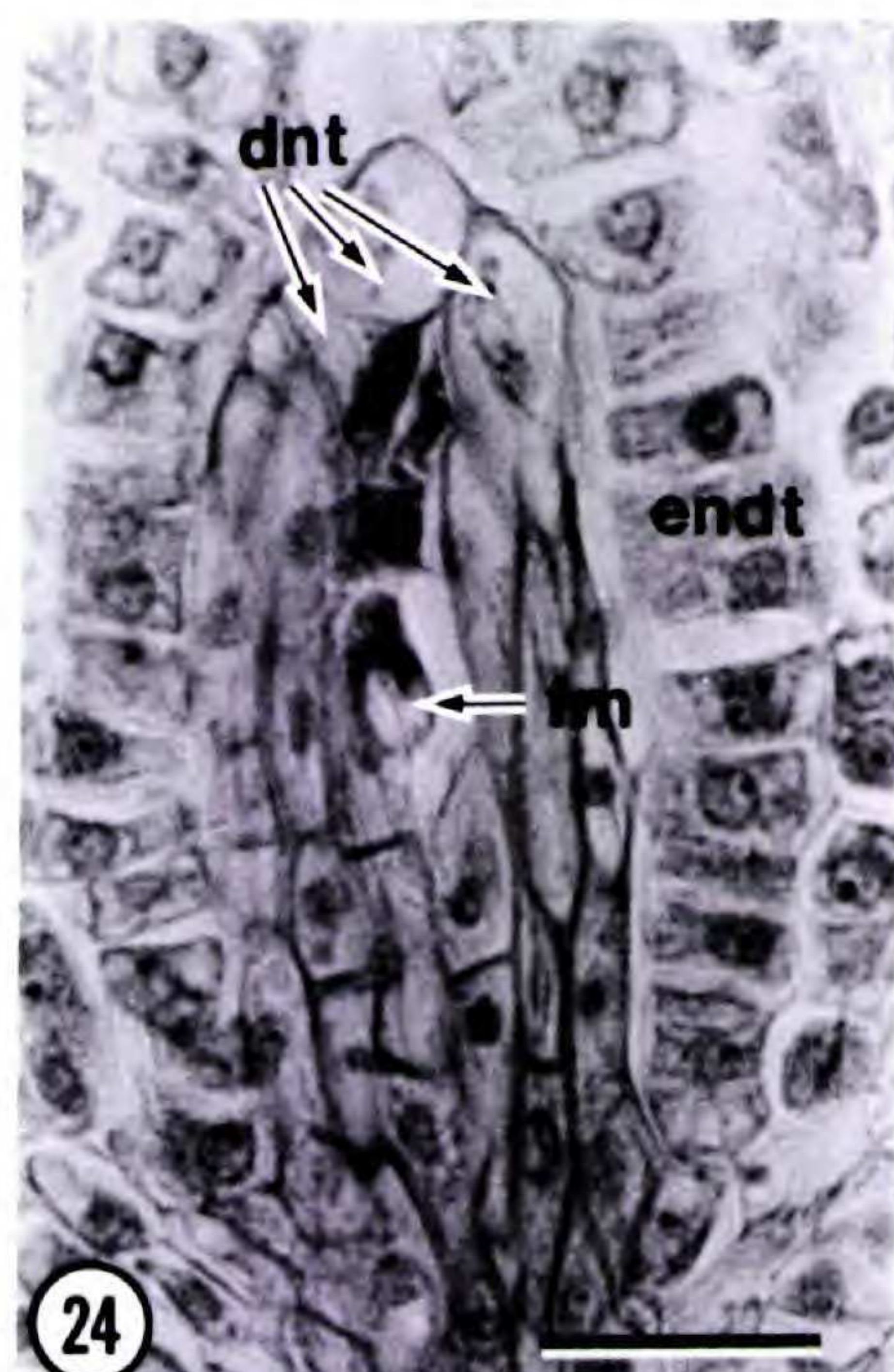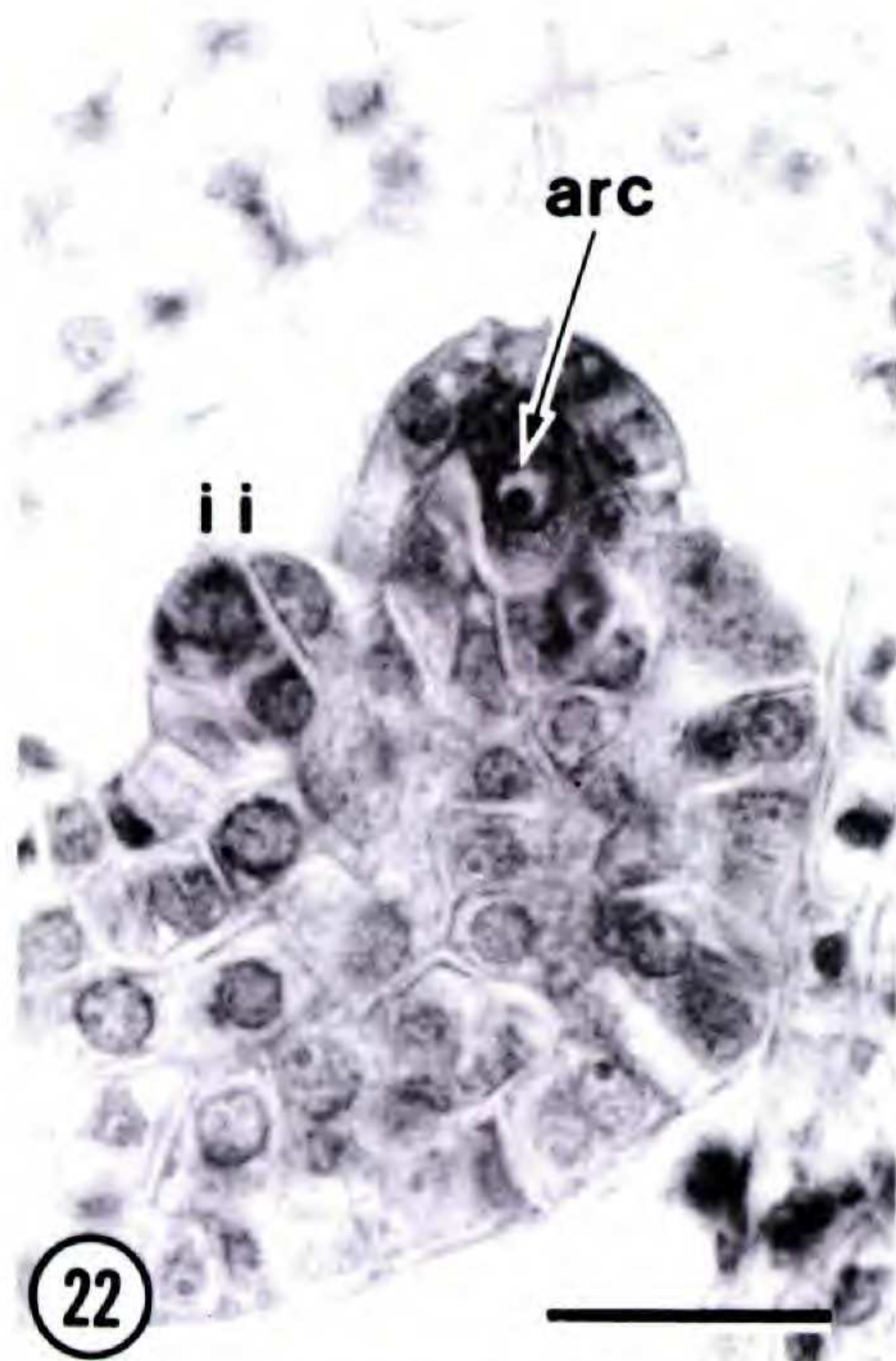
As the nucellar tissue breaks down and the embryo sac comes to border directly on the inner integument, cells of the inner layer of the inner integument become somewhat radially elongated and enlarged (Figs. 24, 28) to form a weakly developed endothelium (i.e., integumentary tapetum).

Fertilization, endosperm, and embryo. Fertilization is porogamous and endosperm formation is nuclear. Wall formation in free endosperm nuclei occurs in later stages, and the young seed is filled with a cellular endosperm. The mature seed is albuminous with copious endosperm (Fig. 31). The endosperm is oily.

Our fruit samples were not adequate to pursue the embryogeny, but based on microtome sections of several proembryos, the embryogeny of *Empleuridium* appears to proceed normally. A suspensor appears to be small and short. The mature embryo is narrow, straight and dicotyledonous (Fig. 31). Both cotyledons develop equally. The mature seed has a large white aril (elaiosome) (Fig. 33) formed by cells derived from the outer integument and probably from the funiculus. It consists of a cushion-like base connected to the micropyle and is drawn distally into coiled filaments. The surface is covered with minute trichomes (Fig. 34).

The seed coat is formed principally by cells of the exotesta and the exotegmen (Figs. 31, 32) that were previously those of the outer layer of the outer and the inner integument, respectively. In the testa, only the cells of the exotesta are persistent and become tanniferous and cuboidal in shape while cells of the remaining part are completely crushed. The cells of the exotegmen are elongate longitudinally and radially, though the longitudinal elongation is more conspicuous,

and become fibrous with pits at places; in addition, cells of the endotegmen that previously formed the endothelium, become slightly elongate longitudinally and tanniferous; cells of all the remaining parts are completely crushed.

POLLEN

The pollen grains are tricolporate, radially symmetric and isopolar, subprolate in lateral view (Figs. 35, 37), and triangular-pleurotreme in polar view (Fig. 36). The surface is reticulate with the widest lumina at the poles (Figs. 35–37). Lumina size decreases toward the equator (Fig. 35) with the smallest lumina around the colpi (Fig. 37). Columellae supporting the muri (i.e., the lumina ridges) are spindle-shaped, unbranched, erect, and with lengths directly proportional to lumina size. Colpi are wide and have a coarse surface. Endoapertures are large, lalongate, and elliptic with rounded ends. The polar axis is ca. 26 μm and the equatorial diameter is ca. 21 μm.

DISCUSSION

RELATIONSHIPS

Empleuridium does not belong in Rutaceae nor to any families in this alliance. It was assigned here when the nature of the gynoecium was unknown and the genus was believed to be dioecious. *Empleuridium* is discordant with Rutaceae in having a nonglandular floral disc; the five stamens alternate with the petals rather than opposite to them; an inferior, non-septate unilocular ovary probably composed of four fused carpels; a single-seeded fruit; and in entirely lacking glands in the leaves and other organs (Cronquist, 1981). At the embryological level *Em-*

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FIGURES 22–30. Development of ovules and megagametophytes in *Empleuridium.* arc, archesporium; mc, megaspore mother cell; fm, functional megaspore; n1 and n2, two nuclei in the two-nucleate embryo sac; n1–n4, four nuclei in the four-nucleate embryo sac; eg, egg apparatus comprising an egg cell and two synergids; cn, central nucleus formed by fusion of two polar nuclei; ii, inner integument; oi, outer integument; endt, endothelium; dnt, degenerating nucellar tissue; mic, micropyle.—22. Longitudinal section (LS) of an ovule primordium at the archesporial cell stage. The archesporium is one-celled. Scale = 20 μm.—23. LS of an ovule primordium at the megaspore mother cell stage showing the tenuinucellate condition. Scale = 20 μm.—24. LS of a young ovule at the megaspore tetrad stage. Note that the tissue of the upper part of the nucellus is degenerating. Scale = 20 μm.—25. LS of a young ovule at the two-nucleate embryo sac stage. Note that the embryo sac directly borders on the inner integument. Scale = 20 μm.—26, 27. Two successive LSs of a young ovule at the four-nucleate embryo sac stage. Scale = 20 μm.—28. LS of a mature ovule with an organized *Polygonum*-type embryo sac. Antipodal cells are not seen because of their ephemeral nature. Scale = 20 μm.—29. LS of a mature ovule showing the micropyle formed by the inner integument alone. Scale = 50 μm.—30. LS of an ovule primordium showing the mode of initiation of integuments. Arrowheads indicate that both the integuments are initiated by oblique-periclinal or periclinal divisions of dermal cells of the ovule primordium. Scale = 10 μm.
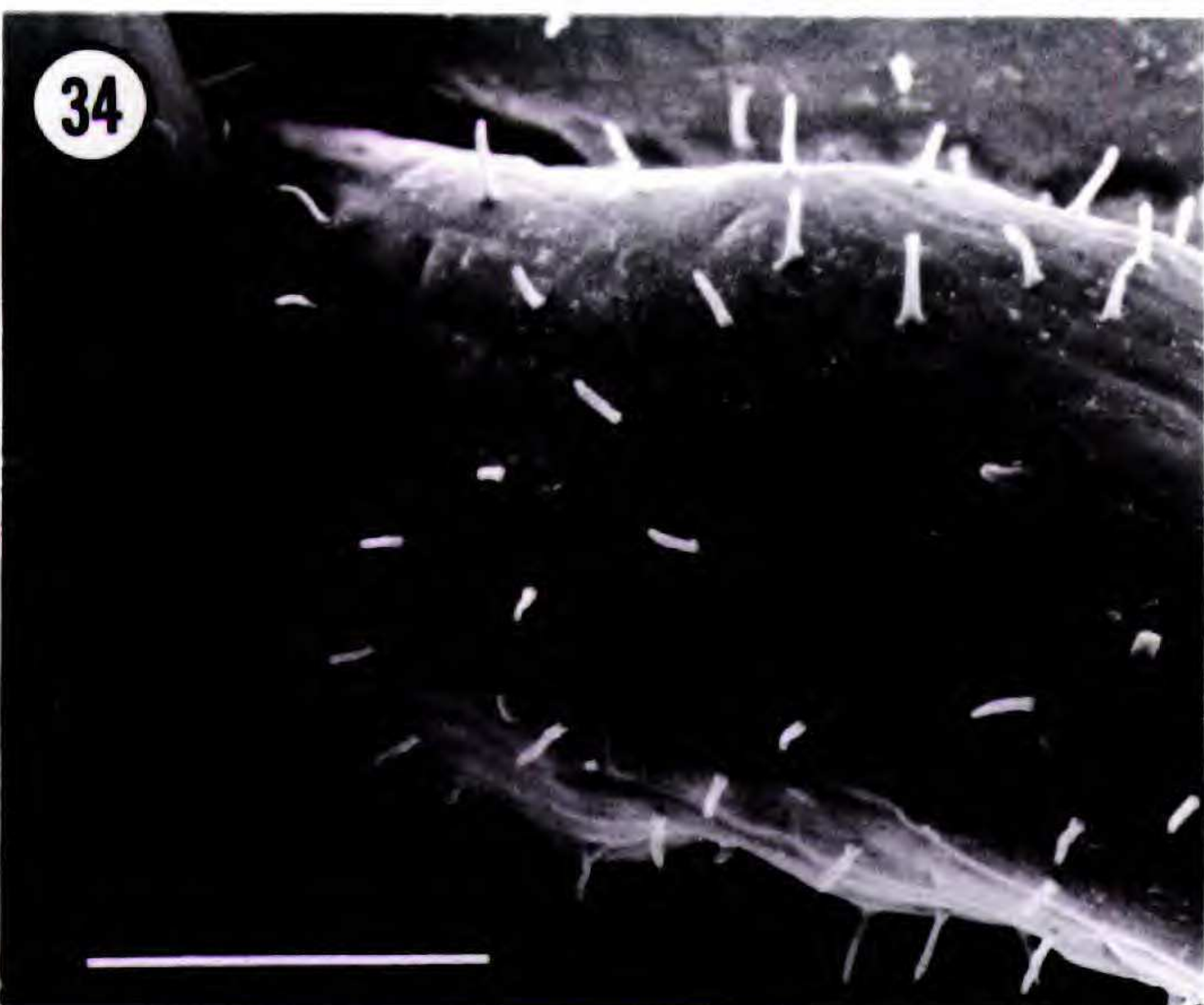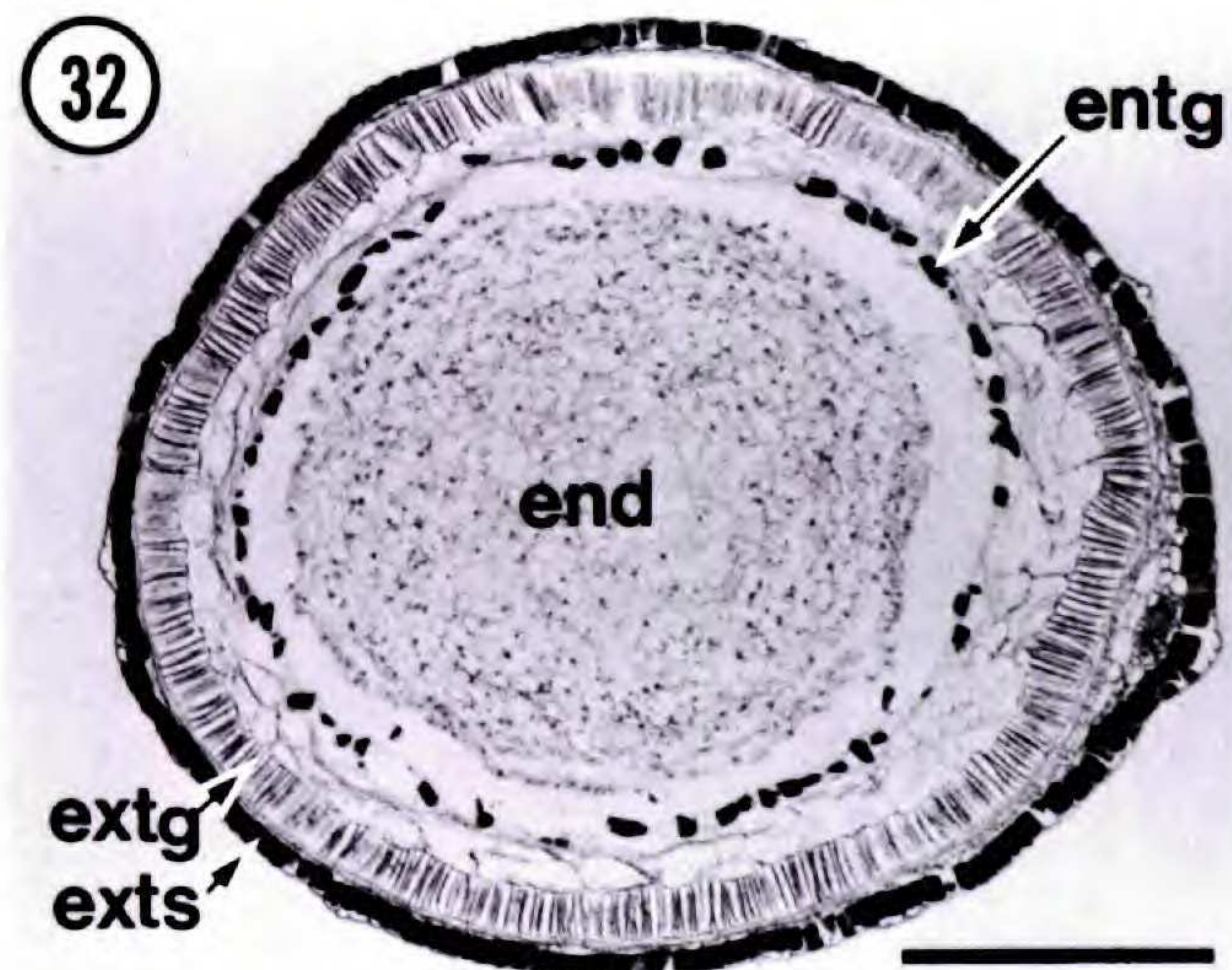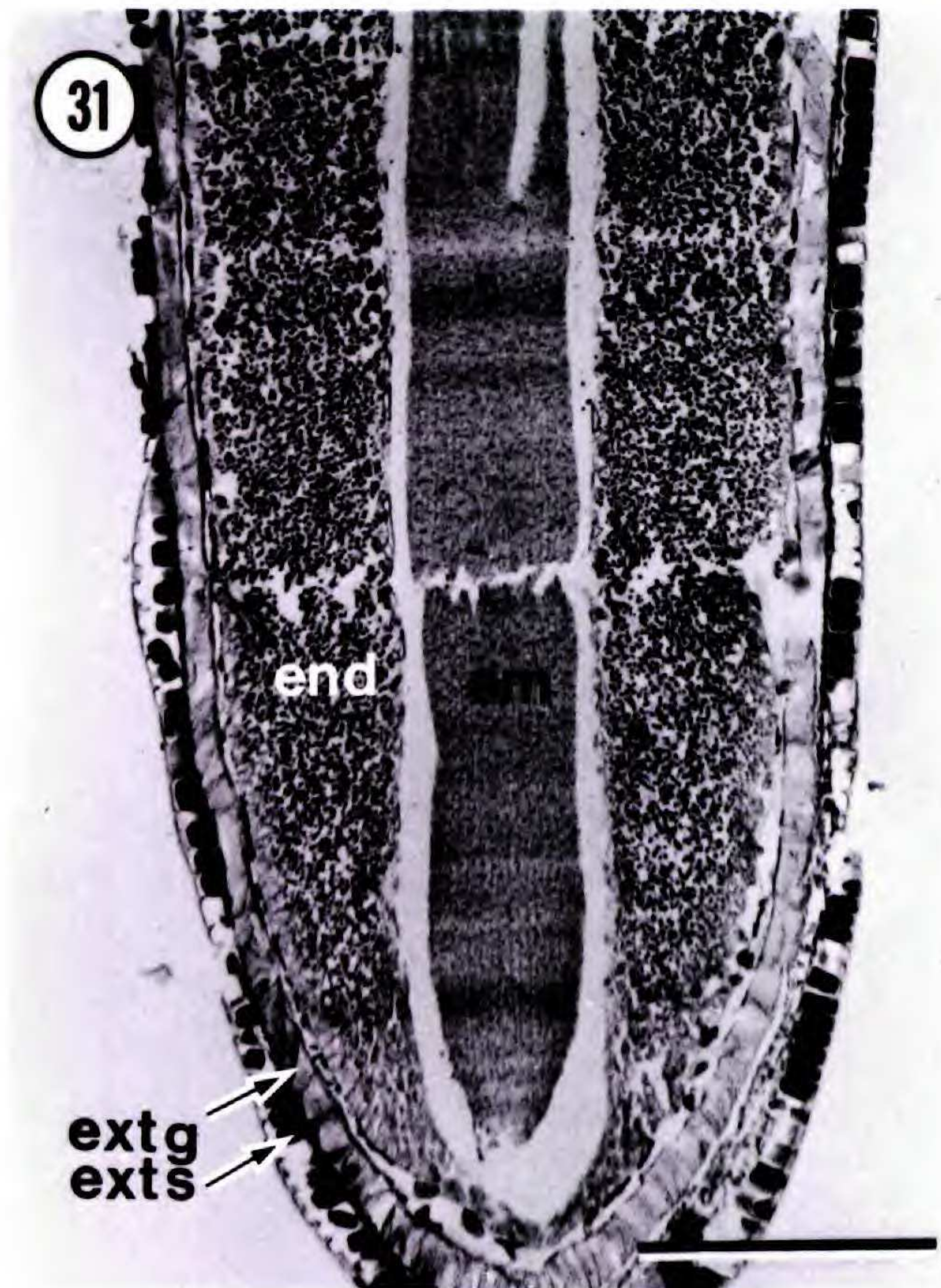
pleuridium contrasts with Rutaceae in having two-nucleate anther tapetum cells in contrast to two multinucleate cells forming polyploid masses by fusion (Johri & Ahuja, 1957; Desai, 1962); a nucellus that degenerates early (persistent in Rutaceae); and the absence of a hypostase (Mauritzon, 1935, 1936; Davis, 1966). Vegetative anatomy also supports the exclusion of Empleuridium from Rutaceae. The wood has tracheids, rather than libriform fibers, and lacks the secretory cavities typical of Rutaceae (Metcalfe & Chalk, 1950).

Morphologically and embryologically, Empleuridium accords well with Celastrales in the broad sense (e.g., Cronquist, 1981), and once its characters are correctly interpreted it keys out to this order in standard keys to the flowering plants. It agrees with Celastraceae in particular, having small bisexual haplostemonous flowers, with a non-secretory floral disc, short filaments and a short persistent style. Embryological characters also accord with Celastraceae, notably the weakly developed and early degenerating nucellus, presence of an endothelium, and the arillate seed with oily endosperm (Berkeley, 1953; Copeland, 1966; Corner, 1976).

The anatomy of Empleuridium is relatively unspecialized. Most of its features are distributed widely in the dicotyledons (ranunculaceous stomata, druses, rhomboidal crystals, tannin cells). The relatively primitive wood with tracheids rather than libriform fibers suggests affinities with several orders with similar wood, e.g., Saxifragales, Rosales, as well as Celastrales. In fact, Empleuridium accords particularly well with Stackhousiaceae, an Australasian group related to Celastraceae, but morphologically very different from Empleuridium and clearly not directly related to it.

The strikingly reticulate surface, subprolate shape, tricolporate apertures, and size of Empleuridium pollen all agree with morphological descriptions of Celastraceae (Erdtman, 1971; Lobreau-Callen, 1977, 1978; Lobreau-Callen & Lugardon, 1972–1973). In personal correspondence with D. Lobreau-Callen, the pollen authority for the Celastrales, Empleuridium is favorably compared with several members of the Celastraceae (viz., Pterocelastrus rostratus, Mystroxylon aethiopicum, Plenckia bahiensis, South African species of Maytenus, and some species of Cassine). A difference with Celastraceae pollen is apparent in the poor development or absence of an endexine fold in the aperture, a character heretofore noted in all members of the family (Lobreau-Callen & Lugardon, 1972–1973). Empleuridium pollen is distinguished within the family (and order) by the reticulum lumina which are larger at the poles than at the equator (see Fig. 35).

Empleuridium is discordant with Celastraceae in its being a low ericoid shrublet, and in floral structure in the inferior unilocular ovary and the micropyle formed from the inner integument alone. It is also unusual in its one-seeded fruit, basal placentation with erect ovules, and the remarkable aril with coiled filamentous extensions. However, in a few Celastraceae the ovary is sometimes nearly inferior (e.g., Paxistima) although usually superior or semi-inferior (Berkeley, 1953); the fruit is occasionally one-seeded (e.g., Bhesa, Plenckia, Zinowiewia, Microtropia) although usually many-seeded (Corner, 1976); and the ovule is sometimes basal and erect (e.g., Euonymus, Behsa, Paxistima) (Berkeley, 1953; Corner, 1976). There is even a comparable seed in the Malaysian Sarawakodendron, in which the aril has branched filaments on the cushion-like base (see Corner, 1976, vol. 2: 81).

Thus, as regards the reproductive characteristics, the difference between Empleuridium and Celastraceae seems to be limited to the non-septate and unilocular ovary and the micropyle formed by the inner integument alone. Even in these features there are examples that reduce the isolation of Empleuridium. In Celastrus orbiculatus Lam. the septa do not fuse in the center of the ovary (Berkeley, 1953), a condition that can be regarded as transitional from (septate) plurilocular to (non-septate) unilocular. The di-

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FIGURES 31–34. Seed and seed coat of Empleuridium. em, embryo; end, endosperm; entg, endotegmen; extg, exotegmen; exts, exotesta; ar, aril.—31. Longitudinal section of a micropylar half of the mature seed containing a straight embryo and the endosperm. Scale = 500 μm.—32. Transverse section of a nearly mature seed. Note the seed coat is formed principally by the exotesta and the fibrous exotesta. Scale = 200 μm.—33. Scanning electron micrograph of the mature seed showing an aril with elaborate structure. Scale = 1 mm.—34. Scanning electron micrograph of a part of the aril. Scale = 100 μm.
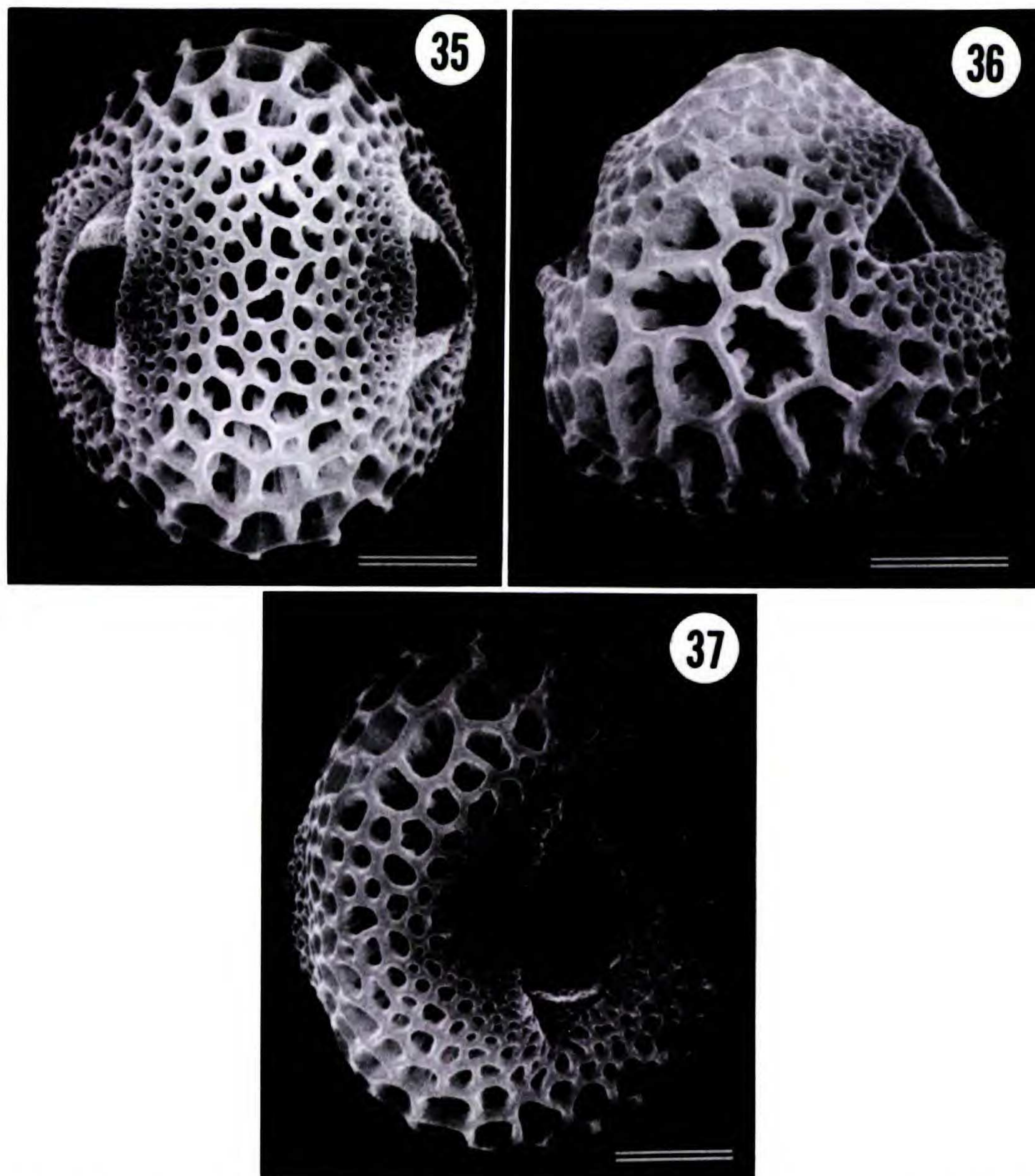
FIGURES 35–37. Pollen of *Empleuridium*.—35. Lateral view. The widest lumina are on the opposite poles with lumina at the equator. Scale = 5 µm.—36. Polar view emphasizing the wide lumina. Scale = 5 µm.—37. Lateral view. Around the margin of the colpus the lumina are greatly reduced. Scale = 5 µm.

versity of ovary structure in the Celastraceae is far from thoroughly studied, and similar trends for carpel fusion and septa reduction may occur in other members of the family, not necessarily closely related to *Empleuridium*. The micropyle of the Celastraceae, however, is formed by both the inner and the outer integuments in all representatives of the family so far examined (Adatia & Gavde, 1962). The number and the kind

of the components of the micropyle is a very important taxonomic character at higher levels, but the significance of the condition in *Empleuridium* should perhaps not be emphasized.

ANATOMY

The very narrow vessels of *Empleuridium* stems, ca. 15 mm in diam., are noteworthy. Few

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FIGURE 38. Morphology of *Empleuridium*.—A. Branch with ripe fruits as well as flowers.—B. Leaf with small subulate stipules.—C. Flower buds.—D. Flower after anthesis, the anthers shed.—E. Flower in even later stage.—F. Same, longitudinally sectioned.—G. Fruit in stage of dehiscence.—H. Fruit, half of the wall removed to show the single arillate seed; the aril is partly removed in the right figure, so that the conical funicle is exposed.—J. Aril, removed and laid open. All from *Esterhuysen 34318* (LD, C). Del. B. Johnsen (orig.).
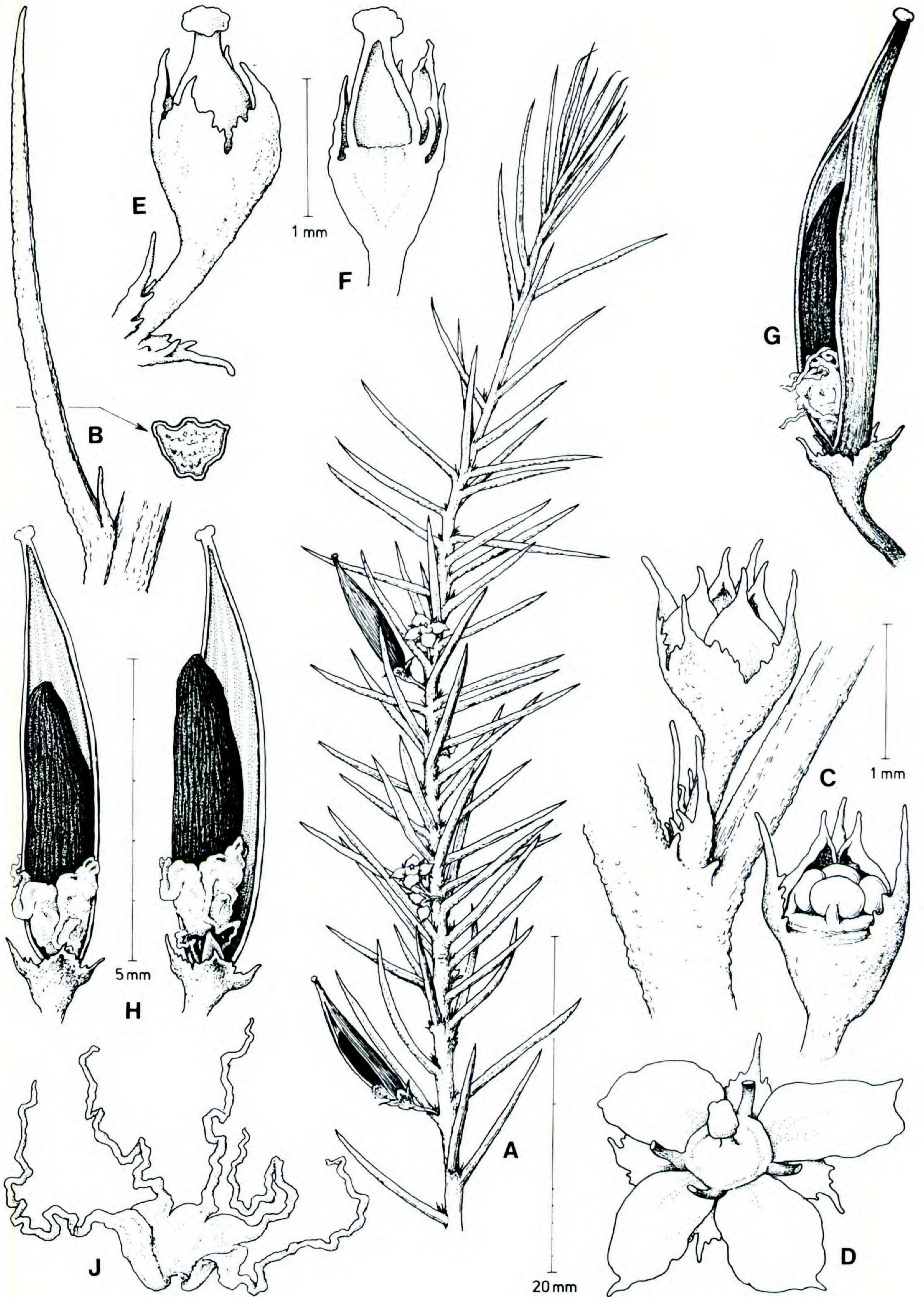
dicotyledons characteristically have vessels this narrow, although Metcalfe and Chalk (1950) reported vessels of about 15 μm diam. in such species as *Bergenia delavayi* (Franchet) Engl. (Saxifragaceae). Vessel elements so narrow, so short, and so numerous per sq. mm of transection as those of *Empleuridium* are clear indicators of xeromorphy (Carlquist, 1977). The wood of the root of *Empleuridium* is somewhat less xeromorphic than that of the stem according to these measures. Wood of roots is generally more mesomorphic than that of stems (e.g., Carlquist, 1978; Carlquist et al., 1983).

The simple perforation plates in the xylem of *Empleuridium* are also an indicator of xeromorphy. Perforation plates with one to three bars, which are occasional in the species, seem relictual of a more primitive condition. They are sufficiently regular in appearance that they cannot be considered a malformation. The scalariform lateral wall pitting on vessels might be a remnant of a primitive condition, although a pseudoscalariform expression (lateral widening of pits based on an ancestry of alternate circular pits) cannot be ruled out.

The occurrence of tracheids in *Empleuridium* wood rather than fiber-tracheids or libriform fibers is a primitive feature in the wood, despite the specialization of perforation plates in vessels. The combination of simple perforation plates in vessels with occurrence of tracheids as the imperforate tracheary element type has been noted as unusually abundant in woods of dry areas, notably chaparral and desert (Carlquist, 1980; Carlquist et al., 1983). The adaptive value of this formulation is the ability to conduct water rapidly during the brief periods when it is available, permitted by simplification of the perforation plates, combined with the safety of tracheids (adapted for conduction, but air embolisms formed under water stress do not spread from one tracheid to another as they do with vessel elements).

The wood of *Empleuridium* is nearly rayless. In dicotyledons at large, raylessness characterizes herbaceous dicotyledons that are undergoing phylesis to woodier stature (Carlquist, 1970). *Empleuridium* is not very woody: it can be described as a diminutive woody herb. The raylessness (or presence of uniseriate rays, composed of erect cells only) in *Empleuridium* can be considered related to its habit. There is so little wood accumulation that one cannot say that this genus is in the process of becoming woodier.

The leaf of *Empleuridium* shows several adaptations to xeromorphy, such as condensed form, thick cuticle, cuticular domes over stomata, and isolaterally distributed chlorenchyma with rather small intercellular air spaces. The presence of unilacunar nodes in *Empleuridium* may also be related to the condensed linear leaves, because many species with linear leaves have unilacunar nodes, even in groups in which broader-leaved species have trilacunar nodes.

SUMMARY

It seems reasonable to assume that *Empleuridium* is a highly specialized member of Celastraceae, and that the unusual features of its flower and fruit are reductions from the basic type for Celastraceae. Clearly its small size, reduced woodiness, and needle-like leaves are specializations comparable with many other examples found in the Cape Flora, where a shrubby microphyllous habit is found in numerous taxa that in many cases have broad-leafed relatives. The specializations in wood anatomy reflect the adaptation to a Mediterranean climate by a small ericoid subshrub, based on a plan compatible with celastraceous woods.

SYSTEMATIC TREATMENT

Empleuridium Sonder in Harvey, Thesaurus Capensis 1: 49. 1859; Flora Capensis 1: 442. 1860; Phillips, Genera S. African Fl. Plants, ed. 1. 353. 1926; ed. 2. 442. 1951; Dyer, Genera Southern African Fl. Plants 1: 292. 1975. TYPE: *E. juniperinum* Sonder & Harvey. Figure 38.

E. juniperinum Sonder & Harvey, Thesaurus Capensis 1: 49–50. 1859; Flora Capensis 1: 442. 1860. TYPE: South Africa. Cape Province: "Bergrucken zwischen Caledon und Babylonschetoorn, 1,000–2,000 ft.," *Ecklon & Zeyher s.n.* (52.8) (S).

Ericoid, erect, glabrous, eglandular, undershrub. Leaves simple, needle-like, scattered, 9–11 mm long, with small scale-like stipules. Flowers axillary, solitary, small, tetramerous, actinomorphic, with a non-secretory receptacular disc, aestivation imbricate; pedicels 1.5–2 mm long, elongating to 3 mm in fruit, with small, paired opposed, scale-like bracts at the base; sepals 4, persistent, ovate, acute; petals alternate to the sepals, whitish, ovate, acute, free, spreading. Stamens 4, opposite the sepals, erect, fila-

ments short, ca. 1 mm long, anthers with 2 thecae, introrse. Ovary hemi-inferior, initially embedded in the receptacular disc, elongating well beyond the level of petal and stamen insertion after anthesis, unilocular, with 4 erect, basal ovules; style short, persistent, stigma capitate. Fruit large, ca. 7 mm long, fusiform, follicle-like, 1-seeded, dehiscing entirely along one suture; seed black, large, ca. 3 mm long, with a large white basal aril (elaiosome).

Distribution. SW Cape, mountains in the Caledon district, mainly above 600 m, on rocky sandstone slopes.

Material examined. 33.19 (Worcester) Blokkop (Aasvogelberg) above Villiersdorp, sun and shade at the rocky summit, ca. 5,200 ft. (CD), *Esterhuysen 35233* (BOL, NBG, S), *35575* (BOL, S).
34.19 (Caledon) Groenland Mts., Mt. Lebanon, 3,600–3,800 ft. (AA), *Goldblatt 6918* (MO); Mt. Lebanon above De Rust, ca. 3,000 ft., local, *Esterhuysen 34318* (BOL, NBG, MO, S); "bergrücken zwischen Caledon und Babylonschetoorn, 1,000–2,000 ft." (?AC), *Ecklon & Zeyher s.n.* (52.8) (S).

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